HERBAGE GROWTH AND UTILISATION UNDER CONTINUOUS STOCKING MANAGEMENT

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DECLARATION

I declare that this thesis has been composed by myself. The field and simulation project described, which were my own responsibility, were carried out within the framework of the grazing studies programme at the Hill Farming Research Organisation. Due recognition of the contributions made by individual members of staff of H.F.R.O. is given in the acknowledgements. Four papers, three of which were written by myself, have been read to conferences and will be published in their proceedings. The texts of these papers are given in appendix 7.

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Mr I.R. Pitkethly did all the photographic work with the exception of plate 3.1, which unfortunately, I am responsible for.

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Miss S. Duncan typed the thesis.

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ABSTRACT

Two field experiments were conducted on a mixed species (*Lolium perenne* L., *Poa annua* L., *Trifolium repens* L.) sward, one in the summer and the other in the autumn of 1979. The objective of the study was to examine the relationship between sward conditions and herbage production. This was done by estimating tissue fluxes in swards maintained as near as possible in a steady state with reference to herbage mass under continuous but variable stocking management with sheep.

In the first experiment four separate swards were maintained at herbage mass levels of 500, 700, 1000 and 1700 kg OM ha^{-1} for the period May to July inclusive. Tissue flows were estimated from measurements on individually identified grass tillers and clover stolons in the field and determinations of tiller and stolon population densities. Rates of herbage growth and senescence compensated each other in such a way that their resultant, net production, was relatively constant over the range of herbage mass from 800 to 1800 kg OM ha^{-1}. Variations within and between treatments in the utilisation of the three plant species were attributable to the distribution of their foliage within the sward canopy. The herbage intake and intake per bite of the ewes increased with the level of herbage mass maintained, but the time the ewes spent grazing increased, reached a maximum in the 1000 kg OM ha^{-1} sward, and then declined as the level of maintained herbage mass was increased.

In the second experiment, deliberate changes in herbage mass

were induced in an attempt to increase the rate of net production above that obtainable in swards maintained at a constant herbage mass. Swards were maintained at either high (1700 kg OM ha^{-1}, HH) or low (700 kg OM ha^{-1}, LL) herbage mass, or manipulated from one state to the other over a period of three weeks in August - September (HL and LH). Rates of growth and senescence compensated each other in such a way that net production was similar in the HH, LL, and LH swards, but in the HL sward rates of herbage growth, senescence and net production were all reduced.

A conceptual model of the sward-animal interface was developed, based upon the results of experiment 1, in which levels of green herbage mass control the rates of herbage growth and senescence, the level of herbage intake and the botanical composition of the diet. A simulation exercise based on this conceptual model was used to examine the implications of basing management decisions on herbage mass or a derivative such as lamina mass. This exercise indicated that lamina was likely to be more useful than herbage mass as the basis for decision making and highlighted the potential of tissue flow analysis as a means of evaluating alternative management systems.

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CHAPTER 1

INTRODUCTION

Management of grazing systems has long been advocated as a means by which levels of pasture production from temperate grasslands can be increased (Smith, 1956 ; Voisin, 1959). The results of both cutting (Brougham, 1959 ; Jameson, 1963 ; Davidson, 1969) and intermittent grazing experiments (Brougham, 1959, 1960) have supported this view by demonstrating that net herbage accumulation is reduced when frequency of defoliation is increased. Hodgson and Wade (1978), however, concluded that net herbage accumulation was relatively insensitive to variations in grazing management or to variations in stocking rate over the range of practical interest and the absence of substantial increases in animal production from intermittent compared to continuous grazing management (Arnold, 1969 ; Marsh, 1976) supports this view. High levels of net herbage accumulation could reasonably be expected to result in higher levels of animal production.

The use of net herbage accumulation as the index of comparison between treatments in both cutting and grazing experiments introduces an almost insurmountable problem to the interpretation of results because net herbage accumulation is the resultant of the processes of growth and decay. Differences in net herbage accumulation between treatments could be due to differences in growth rates alone, differences in decay rates alone, or to differences in both growth and decay rates. In both cutting and grazing experiments, tissue that is not harvested must eventually senesce and die (Vickery, 1981) and therefore the efficiency of harvesting the tissue that has been

grown is a determinant of the level of net herbage accumulation. It is therefore not surprising that cutting and grazing experiments have not produced unequivocal evidence on the influence of grazing management on herbage production.

The objective of the project described in this thesis was to examine the relationship between sward conditions and herbage production. A continuous stocking management was adopted under which animal numbers were manipulated to maintain swards as nearly as possible in a steady state. This allowed tissue fluxes in the sward to be estimated, using an individual plant unit measurement technique, against a background of minimal net change in sward conditions.

Two field experiments were conducted to determine patterns of tissue flow, one when herbage mass was maintained in steady state and one when it was manipulated from one state to another. A simulation exercise, based upon a conceptual model derived from the results of these two experiments, was used to examine patterns of tissue flow throughout a grazing season.

CHAPTER 2

REVIEW OF LITERATURE:

FACTORS AFFECTING TISSUE FLOW

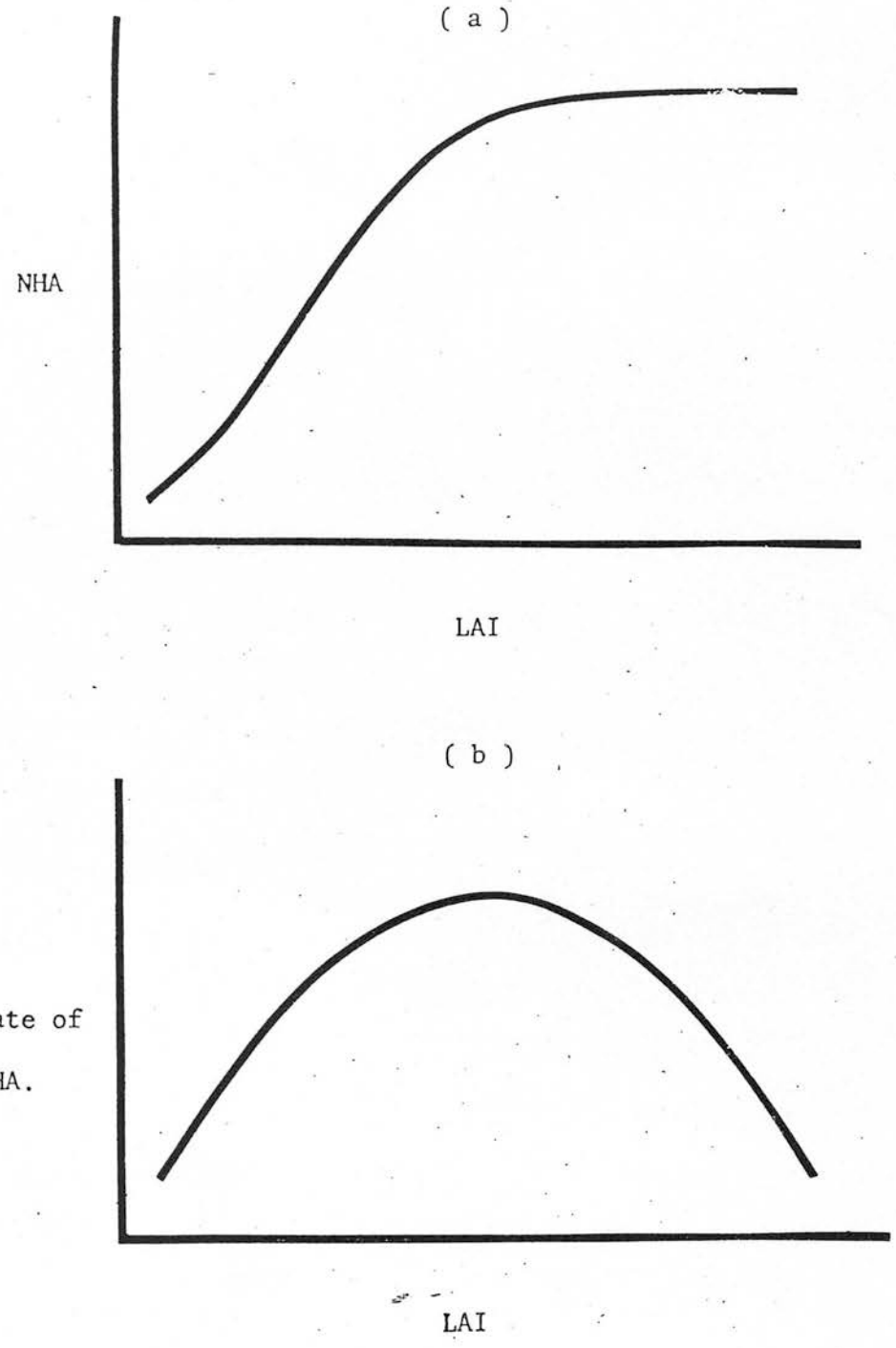

Figure 2.1.1. (a). The logistic relationship between net herbage accumulation (NHA) and leaf area index (LAI) over time. (b). The relationship between rate of net herbage accumulation and leaf area index assuming (a).

2.1 INTRODUCTION

It appears to be generally accepted that net herbage accumulation decreases as frequency of defoliation increases (Brougham, 1959 ; Jameson, 1963 ; Davidson, 1969) though for some species, usually of prostrate habit, net herbage accumulation increases as frequency of defoliation increases (Davidson, 1969). These differences can probably be reconciled by recognition of the effects of harvesting efficiency on level of net herbage accumulation (Tayler and Rudman, 1966 ; Anslow, 1967).

Intermittent grazing managements, in which frequency of defoliation is controlled, have been advocated (Brougham, 1970) in preference to continuous grazing management because it has been assumed that frequency of defoliation is lower in the former than the latter. Support for the view that intermittent grazing must be better than continuous grazing has also come from general acceptance of a logistic relationship between net herbage accumulation and leaf area index (figure 2.1.1) over time during uninterrupted regrowth (Brown and Blaser, 1968). It has been assumed that the low rates of net herbage accumulation measured in intermittently grazed swards of low leaf area index would also occur in continuously grazed swards which typically have a low leaf area index.

In view of the general acceptance of the logistic relationship and the consequent existence of an optimum leaf area index (figure 2.1.1) at which the rate of net herbage accumulation is maximal (Davidson and Donald, 1958), it is surprising that net herbage accumulation has not been found to at first increase and then decrease with increasing frequency of defoliation. It may be that all frequency of defoliation experiments have been conducted at leaf area index levels less than the optimum in which case net herbage accumulation would decrease with increasing frequency of defoliation but this seems unlikely. Clearly other factors are involved in this response which net herbage accumulation as the index of comparison is unable to represent because it is the resultant of tissue flow into and out of sward.

The tissue flow approach to the study of grazing management has been described by Bircham (1980), Bircham and Hodgson (1981) and Hodgson, Bircham, Grant and King (1981). Hodgson et al (1981) reviewed the factors which influence tissue flow.

In the absence of the grazing animal the tissue flow model is described by equation 2.1.1

$$NHA = G - D \quad \ldots \quad 2.1.1$$

where 'NHA' is the rate of net herbage accumulation, 'G' is the rate of growth of new tissue and 'D' is the rate of loss of mature tissue to decomposition. In the presence of the grazing animal, rate of net herbage accumulation is also influenced by the rate of

herbage consumption 'C' (equation 2.1.2).

$$NHA = G - (D + C) \quad \ldots \quad 2.1.2$$

The units of both equations can be either per unit area per unit time or per individual plant unit per unit time. For grasses this individual plant unit could either be a genet or an individual tiller of a genet. Equally, for a stoloniferous legume such as white clover, the individual plant unit could either be a genet (an entire stolon - axillary branches included) or an aggregation of active buds (a growing point).

Very few studies have been conducted on temperate grassland in which the growth and decay or senescence (an alternative to decay, see section 3.1) components of tissue flow have been determined (Morris, 1970 ; Hunt, 1970 ; Simons, Davies and Troughton, 1972 ; De Lucia Silva, 1974 ; Tainton, 1974 ; Williamson, 1976 ; Wilman and Mares-Martin, 1977 ; Davies and Simons, 1979 ; Wade, 1979 ; Cayley, Bird, Watson and Chin, 1980). Of these studies, three were grazing experiments (De Lucia Silva, 1974 ; Tainton, 1974 ; Cayley et al, 1980) and a fourth was conducted on ungrazed chalk grassland (Williamson, 1976), the remainder being cutting studies.

Higher levels of both growth and senescence occurred in simulated continuously grazed swards maintained at a leaf area index of 4.6 compared to 3.8 (Morris, 1970). However, harvested yield was higher in the leaf area index 3.8 sward. Under grazing, Tainton (1974) found that net herbage accumulation was maximised in

the treatment which minimised losses through decomposition, growth rates being similar in all treatments.

It is possible in grazed temperate swards that net herbage accumulation is relatively constant over a range of managements and stocking rates (Hodgson and Wade, 1978) because variation in the growth and decay (senescence) components of tissue flow tend to compensate each other. For example, high growth rates are associated with high leaf area index (Morris, 1970) but so too are high senescence rates (Morris, 1970 ; De Lucia Silva, 1974 calculated by Wade, 1979).

The remainder of this chapter is devoted to a brief review of the factors that influence tissue flow in grazed swards and the susceptibility of these factors to manipulation by management. Thus growth and senescence, plant species competition and its resultant population density, and intake per animal are considered. The effects of nutrient and water supply on these factors are not specifically considered but are occasionally referred to in passing.

2.2 GROWTH AND SENESCENCE

Factors affecting the growth of leaves are of considerable importance because leaves as the primary organs of photosynthesis can account for 0.95 of the total CO_2 fixed in a grazed sward (Leafe, Parsons, Stiles and Collett, 1978). Leaf growth commences with cell division in the leaf primordium and is only visible when the lamina appears at the ligule of the previous leaf. Prior to emergence the leaf is almost entirely dependent upon assimilate provided by the rest of the plant but subsequently is able to produce photosynthate of its own. The photosynthetic capacity of successive newly expanded leaves of perennial ryegrass in an undisturbed sward falls dramatically (Woledge and Leafe, 1976) almost certainly as a direct result of shading during expansion (Woledge, 1978). Similar leaves on reproductive tillers have high photosynthetic capacities because stem extension carries them to the top of the canopy where they are well illuminated during expansion (Woledge, 1979). Leaves in continuously stocked hard-grazed swards have and retain high photosynthetic capacity because a low leaf area means less mutual shading of leaves, developing leaves emerge into full sunlight and older leaves remain relatively well illuminated (Leafe et al, 1978).

Rate of leaf appearance has been reviewed by Anslow (1966) and Silsbury (1970). Appearance rates increase with temperature up to 25° for grasses (Anslow, 1966) but the response is variable

according to species, and at low light intensity the influence of temperature can be minimal (Silsbury, 1970). Reduced light intensity generally reduces rate of leaf appearance but nutrient supply has little apparent effect (Anslow, 1966). Leaf appearance rate slows as tiller size increases (Robson, 1973 ; Robson and Deacon, 1978) and ultimate lamina size is related to the level of insertion on the shoot. During uninterrupted growth, rate of leaf appearance decreases and the size of successive laminae increases (Silsbury, 1970) until the crop reaches ceiling yield.

In grasses, decreased light energy levels generally increase laminae area and reduce the specific leaf area (Silsbury, 1970) producing longer, thinner and narrower laminae. Leaf expansion is reduced at high temperatures (Silsbury, 1970). Cell and leaf expansion are both very sensitive to water stress with even small water deficits reducing expansion in some species, but photosynthesis is not as sensitive and dry weight accumulation can continue after the cessation of expansion (Hsiao, 1973).

The general pattern of dry matter increase over time of the emerging leaf is sigmoid shaped (figure 2.1.1) and for ryegrass laminae there is a substantial period during which dry weight accumulation increases linearly (Silsbury, 1970). After the attainment of maximum dry weight, lamina weight declines until leaf death at which time in perennial ryegrass it is of the order of 0.3 - 0.4 of the maximum weight previously achieved (Vine, 1977 ;

Robson and Deacon, 1978).

Dry weight accumulation on a whole sward basis in both seedling and established swards is also sigmoid in shape (Brougham, 1956 ; Robson, 1973). However, the sigmoid curve of whole sward dry weight accumulation does not describe growth in the same way as the sigmoid curve for an individual leaf, because it is the resultant of both growth and decay. Frequently rate of dry weight accumulation on a whole sward basis (net herbage accumulation) is referred to as the growth rate of a sward but this is inaccurate (equation 2.1.1).

Rate of senescence is usually increased by shading, high temperature, moisture deficits and restricted water supply (Leopold, 1964) and, since the number of leaves on a grass tiller is more or less constant (Anslow, 1966), senescence rate in an undisturbed sward is correlated with the rate of leaf appearance. Thus higher rates of senescence can be expected in leniently than in severely defoliated swards (Morris, 1970) because more tissue remains after defoliation which must eventually senesce and die (Vickery, 1981).

2.3 PLANT SPECIES COMPETITION

Grime (1974, 1977) proposed a triangular ordination model which interrelates the effects of competition, stress (nutrient or moisture stress etc.) and disturbance (defoliation or anything

that destroys aerial tissue) on botanical composition. Grime (1973) defined competition between plants as the tendency of neighbours to utilise the same quantum of light, ion of a mineral, molecule of water or volume of space.

Plant species that are competitive have attributes conducive to the efficient capture and utilisation of light, water, mineral nutrients and space (Grime, 1974). An elevated leaf canopy, for example, would aid the capture of light. Plant species that are stress tolerant are usually small in stature and have low potential relative growth rates compared to species exhibiting either competitive or ruderal strategies (Grime, 1974). Plant species that exhibit ruderal strategies are usually found in disturbed habitats and are frequently annuals or short lived perennials (Grime, 1974). It is therefore not surprising that ruderal species have a capacity for rapid establishment, growth and seed formation (Grime, 1977). Obviously disturbance can alter the balance between competitive species and severe disturbance will alter the balance of species towards those of a ruderal type.

In demographic terms (Harper and White, 1974), a good pasture management can be defined as that which aids the recruitment and persistence of desired species. Conversely, a poor management can be described as that which hastens the death of preferred species and/or aids their replacement by inferior species (Jones and Mott, 1980). Jones (1933 a, b) and Harris and Brougham (1968) have

demonstrated the influence of grazing management on the botanical composition of a sward. Thus, Harris and Brougham (1968) demonstrated ingress of Agrostis tenuis Sibth. into a perennial ryegrass - white clover sward under continuous hard grazing but not under more lenient rotational grazing. The ingress of Poa annua L. into established swards often follows intensive grazing, particularly in areas where soil compaction and poaching have made the environment less favourable for sown species (Wells, 1974 a). Harris (1978) referring to the Palmerston North, New Zealand, environment observed that rotational grazing with a high level of pasture utilisation generally resulted in a simple ryegrass - white clover mixture. Ingress of taller species occurred at lower levels of utilisation and close , continuous defoliation led to a more species-rich association dominated by prostrate, rhizomatous, stoloniferous or basal rosette habits. When defoliation was particularly severe, ingress of annuals occurred.

Pasture composition changes induced by changes in defoliation frequency and intensity when nutrients and water are not markedly limiting can largely be explained by light relationships within the canopy (Harris, 1978), defoliation allowing light to penetrate to the leaf canopy of the more prostrate species and restricting the ability of taller growing species to shade prostrate species. However, nutrients and moisture are rarely non-limiting and can have a marked influence on the competitive ability of species.

2.4 SPECIES POPULATION DENSITY

The outcome of competition, which is the resultant of the recruitment and death of plant units, is the population density of a species.

The population density of grass tillers is unlikely to be limited by the supply of tiller buds (Davies, 1977) but, in the absence of defoliation, tiller initiation can be inhibited by low light intensity (Davies, 1977). Tiller death can be increased both by severe shading (Kays and Harper, 1974) and by severe defoliation (Brougham, 1959). Tiller population densities tend to increase as frequency of defoliation increases (Hodgson et al, 1981) and are usually maintained at a higher level under continuous than under rotational grazing at comparable stocking rates (Hodgson and Wade, 1978). Grazed swards appear to conform to the negative exponential relationship between population density and individual plant unit weight (Yoda, Kira, Ogawa and Hozumi, 1963) with the relationship breaking down at very low herbage mass (Hodgson et al, 1981). The smallest tillers are the most vulnerable and likely to die when a whole plant is stressed (Ong, 1978), and death in these circumstances is often due to favourably placed tillers not supporting those that are severely shaded (Ong, Marshall and Sagar, 1978). Defoliated tillers can import substrate from undefoliated tillers, but reproductive tillers retain most of the carbon they fix, thus predisposing associated stressed tillers to death (Ong et al, 1978).

Seasonal patterns of population density may be relatively unaffected by management (Tallowin, 1981) with periods of rapid tillering in grasses often occurring both before and after flowering (Langer, 1963). In the opinion of Grant, King, Barthram and Torvell (1981), differences in population density related to grazing management may be more evident after the summer solstice than before it.

2.5 INTAKE PER ANIMAL

Herbage consumption per unit area is the product of intake per animal and stocking density. These two components interact and herbage intake per animal falls as stocking density increases in response to a reduction in herbage mass and to a reduction in the nutritive value of the diet (Hodgson, 1975). Sward conditions can affect intake per animal independently of stocking density (Hodgson, 1977).

Herbage intake in large herbivores has been recently reviewed by Van Dyne, Brockington, Szocs, Duek and Ribic (1979) and Freer (1981) has reviewed the control of food intake by grazing animals. Herbage intake declines from an asymptote level at an increasing rate below a critical level of herbage mass and this critical level can vary between animal species and between sward types (Hodgson, 1975, 1977). Differences in critical mass levels may be attributable

to differences in sward structure and the reaction of the grazing animal to that structure. Thus rate of intake can decrease as the height of the grazed horizon approaches the soil surface (Hodgson, 1977). Herbage intake can also decline as the grazed horizon approaches pseudostem height (Barthram, 1980).

The effects of sward structure (as described by sward height for example, or leaf bulk density) on herbage intake are mediated by the grazing animal and can be described in terms of their grazing behaviour. Thus animals unable to maintain intake per bite at the same level as that previously possible may attempt to compensate for this reduction by increasing the time spent grazing (Allden, 1962 ; Arnold, 1964 ; Allden and Whittaker, 1970 ; Jamieson and Hodgson, 1979 a) and occasionally by also increasing the rate of biting (Allden and Whittaker, 1970 ; Jamieson and Hodgson, 1979 a). The system of management imposed upon grazing animals can also influence their grazing behaviour response (Jamieson and Hodgson, 1979 b).

In tropical swards the correlation between intake per bite and leaf bulk density is positive (Stobbs, 1973, 1975 ; Chacon and Stobbs, 1976) and it has been suggested that animals grazed on such swards react primarily to the lamina present in the grazed horizon (Stobbs, 1973, 1975 ; Hendricksen and Minson, 1980). In temperate swards, however, the correlation between intake per bite and sward height is better than the correlation between intake per bite and

leaf bulk density (Allden and Whittaker, 1970 ; Hodgson, 1981).

The digestibility of a forage diet is generally accepted as a measure of nutritive value and an index of voluntary intake (Hodgson, 1977). Digestibility values for temperate grasslands are rarely less than 0.45 - 0.50 or greater than 0.85 (Corbett, 1978) and linear relationships between voluntary intake and digestibility occur over a wide range of herbage diets (Freer, 1981).

Grazing animals eat green leaf in preference to dead leaf or stem tissue (Arnold, 1981 ; Dudzinski and Arnold, 1973), but animal preference for different species in improved temperate grassland swards is less well established although plant genotypes of high compared to low alkaloid content are avoided by both sheep and cattle (Marten, 1978). Curll and Wilkins (1980) demonstrated that the proportion of clover in the diet was greater than the proportion of clover present in the sward. Milne, Hodgson, Souter and Barthram (1981) obtained similar results but when the proportion of clover in the diet was compared to the proportion of clover in the grazed horizon, there was no evidence of preferential grazing of clover.

2.6 TISSUE FLOW IN A GRAZED SWARD

Tissue flow in a grazed sward is the resultant of many interacting processes. Thus the light regime to which a young

expanding leaf is exposed affects its current and subsequent photosynthetic capacity (Woledge, 1977). Also, the amount of leaf tissue harvested from a plant unit affects not only subsequent growth rates, through reduced leaf area and perhaps reduced photosynthetic capacity of residual leaf, but also subsequent rates of senescence and decay because unharvested tissue must eventually die (Vickery, 1981). Intraspecific and interspecific competition between plant units determines the population density of a species and the product of population density and tissue flow on individual plant units determines tissue flow per unit area. Competition also determines the position of a plant unit relative to that of other plant units within a canopy and this relative position determines whether a plant unit is shaded with consequent effects on the photosynthetic capacity and growth of leaves. This relative position also determines whether a plant unit is as accessible as other plant units for harvesting by the grazing animal with consequent effects on senescence and decay. The botanical composition of the diet selected by the grazing animal affects competition between plant units by altering canopy structure with consequent effect on canopy light regimes etc.. Increasing stocking density by reducing the opportunity for the grazing animal to select a preferred diet can also influence canopy structure with consequent effect on plant unit competition and tissue flow.

It is not surprising that net herbage accumulation as the index of comparison has failed to produce unequivocal evidence

on the influence of grazing management on herbage production. The fact that net herbage accumulation is the resultant of the processes of growth, decay and consumption in a sward, and that these processes in turn are the resultant of other processes such as plant competition and the behaviour of the grazing animals, makes this inevitable. Compensatory changes in the growth and decay components of net herbage accumulation may of course occur and this would be consistent with the conclusion of Hodgson and Wade (1978), that net herbage accumulation is relatively constant over a range of managements and stocking rates. Analysis of the flow of tissue in a sward is a means by which the influence of sward conditions on herbage production can be assessed.

Tissue flow analysis was used in two field experiments to determine the influence of sward conditions on herbage production and utilisation.

CHAPTER 3

EXPERIMENT 1

3.1. INTRODUCTION

In this experiment, mixed species swards of different herbage mass were established and maintained in as near steady state as possible (NHA = 0) by continuous but variable stocking with sheep. In this circumstance equation 2.1.2. can be transformed to equation 3.1.1

$$NP = G - D = C \quad \ldots \quad 3.1.1$$

where net production of herbage (NP), the balance of growth and decay, is equal to consumption. The measurement of 'D' is difficult and an alternative is to measure senescence (S), the rate at which live tissue becomes chlorotic so that equation 3.1.1 becomes equation 3.1.2.

$$NP = G - S = C \quad \ldots \quad 3.1.2$$

The objectives of maintaining the swards in as near steady state as possible were twofold in that (1) not only is it possible to relate the many aspects of the sward-animal interface to a common parameter, herbage mass, but also (2) to examine the concept that net herbage production in a mixed species sward is relatively constant over a range of herbage mass. This concept appeared consistent with the views expressed by Hodgson and Wade (1978) and was examined in experiment 1 which was conducted during the summer of 1979.

Plate 3.1. The Hard Park Field, 1979.

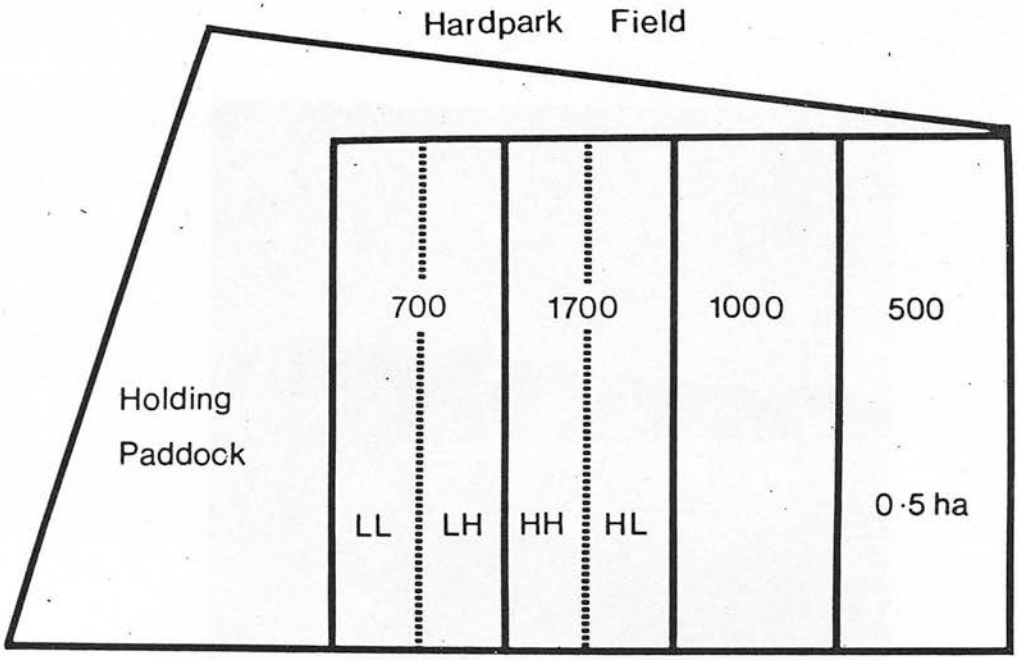

Figure 3.2.1 The experimental layout for experiment 1 , 700, 1700, 1000 and 500 paddocks ; and the layout for experiment 2, LL, LH, HH and HL.

The experiment was conducted on the Hard Park field of the Hill Farming Research Organisation, Glensaugh Farm situated on the eastern side of the Grampians, Kincardineshire, Scotland.

3.2. MATERIALS AND METHODS

3.2.1. HISTORY OF THE EXPERIMENTAL AREA

The Hard Park field had been cultivated and reseeded with Lolium perenne L. and Trifolium repens L. in 1972 and for the 4 years prior to the commencement of experiment 1, the field (plate 3.1) was part of an intensive stocking upland sheep systems experiment (Anon, 1979). During this time ingress of Poa annua L. occurred. After the severe winter of 1978/79 when snow lay on the field for 3 - 4 months until April 1979, the sward was sparse in places but after fertiliser application responded rapidly and was ready for the commencement of the experiment in May 1979.

3.2.2. EXPERIMENTAL DESIGN AND SWARD MANAGEMENT

Fertiliser (N = 123 kg ha^{-1}, P = 37 kg ha^{-1}, K = 37 kg ha^{-1}) was applied in mid-April.

Four 0.5 ha paddocks were established and the four treatments (figure 3.2.1) allocated at random without replication. The levels of herbage mass, originally intended to span the range from over to under stocking, were 500, 800, 1200 and 1700 kg OM ha^{-1}. The actual

Plate 3.2. The four treatment swards.

' 500 '

' 700 '

' 1000 '

' 1700 '

levels achieved by grazing down or allowing the sward to grow were 500, 700, 1000 and 1700 kg OM ha^{-1}. It proved difficult to graze down an already prostrate low mass sward to a level of 500 kg OM ha^{-1}, and to overcome this difficulty the sward was allowed to grow to a level of 700 - 1000 kg OM ha^{-1} and then mob stocked with wethers until the 500 kg OM ha^{-1} mass was achieved. Continuous grazing with ewes and single lambs commenced on the 20th April, 4th May, 25th May and 25th May for the 700, 1000, 500 and 1700 kg OM ha^{-1} swards respectively and continued through until weaning in late July. After weaning, the swards were continuously grazed with ewes only.

Once the desired levels of herbage mass had been achieved the stock adjustments necessary to maintain the swards in as near steady state as possible were controlled by measurements of sward surface height which were taken twice weekly (section 3.2.5.2). Core flocks of 5 - 6 ewes plus single lambs were maintained continuously on each sward and additional ewes and lambs used to make the necessary adjustments. It was realised that the herbage height and herbage mass relationship was unlikely to remain constant throughout the reproductive phase of sward growth but this was the only rapid, objective and practical method of assessment available.

The four swards are depicted in plate 3.2.

3.2.3. STOCK MANAGEMENT

Mature 3 year old Greyface (Border Leicester x Scottish Blackface) ewes with single lambs by a Dorset Down ram were weighed (non-fasted) and allocated to each sward such that mean treatment

liveweights were initially equivalent. Similar ewes fistulated at the oesophagus and also with single lambs were grazed alongside the treatment ewes. All ewes were fed a supplement until the 11th May when all supplementary feeding ceased. Clipping of the ewes and weaning of the lambs was undertaken in late July when the experimental measurements were completed.

As was expected, ewe liveweights on the 500 kg OM ha^{-1} sward fell rapidly and any ewe whose liveweight fell below 50 kg was removed and replaced. As soon as the experiment proper was completed the 500 kg OM ha^{-1} sward was stocked by wethers.

3.2.4. EXPERIMENTAL MEASUREMENTS - GENERAL

Measurements of sward height, herbage mass and sheep liveweight were made at regular intervals throughout the grazing season. In addition there were three 2-week periods of intensive measurement when detailed measurement of sward and animal parameters were made. These intensive measurements were conducted in May (14-25th), June (11-21st) and July (2-16th). The first period (May) was used to establish the field techniques which were made on the 700 kg OM ha^{-1} sward only. The intensive measurement periods in June and July are regarded henceforth as periods 1 and 2 respectively.

Plate 3.3. The apparatus used to measure sward surface height.

3.2.5. SWARD MEASUREMENTS

3.2.5.1 Herbage Mass

Ground level cuts using Sunbeam shearing hand-pieces and 1.22m x 0.15m quadrats were made every two weeks throughout the grazing season. Four quadrats per quarter and 16 per paddock were taken, 8 per operator. The 16 samples were individually dried and weighed and samples bulked on an operator basis for determination of organic matter content.

3.2.5.2 Herbage Height

The surface height of undisturbed herbage was measured twice a week using the apparatus depicted in plate 3.3. The perspex slide was lowered until the first contact on undisturbed foliage was made and the height of this point above the soil surface recorded. Five pairs of measurements per quarter (40 values per paddock) were used to determine the mean surface height of herbage.

Because the intensity and frequency of sampling sward surface height was greater than that for herbage mass, a regression equation relating herbage mass (HM - kg OM ha^{-1}) to sward surface height (H - cm) was derived (equation 3.2.1).

$$HM = 56.8\ (\pm 86.5) + 381.6\ (\pm 52.3)\ H - 18.9\ (\pm 6.0)\ H^2 \qquad \ldots\ 3.2.1$$

$$R^2 = 0.92^{***},\ n = 52.$$

Mean sward surface height was used to calculate mean herbage mass for the period using this equation.

3.2.5.3 Species Population Density

The population densities of grass tillers, clover growing points and weed stems were determined once in every intensive measurement period from (10.0cm x 5.0cm) quadrats cut to ground level from three 20cm x 20cm x 10cm turf samples per quarter paddock. These samples were taken from the field for analysis in the laboratory. All the visible daughter tillers were counted. A growing point for clover was defined as an aggregation of two or more petioles associated with active stolon formation.

3.2.5.4 Horizon Herbage Mass

Horizon herbage mass was determined on a total and species basis by sampling in 2cm deep horizons from (10.0cm x 5.0cm) quadrats in the laboratory. Turf samples were taken from the field (two per quarter) as for population density estimation. Each horizon was botanically separated into grass, clover, weed, detached dead and seed head, the components dried for 24 hours at 80°C and then weighed. Samples from the 0 - 2cm horizon were washed in water prior to separation and drying.

In period 2 only, herbage was further separated into green lamina, green stem and dead tissue (attached and detached).

3.2.5.5 Leaf Area

Herbage samples taken from the field were frozen for later leaf area determination. The characteristic folding of leaves that occurs when frozen samples are thawed was overcome by floating the lamina in tepid water and then rapidly drying the leaves on filter paper.

The areas of individual grass laminae (20 per treatment) were determined from lamina length and mid-rib breadth measurements and also from direct planimetric measurements using an electronic planimeter. The relationships between these two estimates of leaf area were determined by regression analysis using planimetric area (A) as the dependent variate and length by breadth estimated area (LB) as the independent variate for both ryegrass (equation 3.2.2.) and Poa (equation 3.2.3.).

$$A = 1.56\ (\pm 1.43) + 0.83\ (\pm 0.03)\ LB, \qquad \ldots\ 3.2.2.$$
$$R^2 = 0.89^{***},\ n = 80.$$

$$A = 2.50\ (\pm 0.79) + 0.76\ (\pm 0.02)\ LB, \qquad \ldots\ 3.2.3.$$
$$R^2 = 0.94^{***},\ n = 80.$$

The ranges of the LB estimates of leaf area were 4 - 110 mm^2 and 5 - 85 mm^2 for ryegrass and Poa respectively.

Clover trifoliate leaf area was estimated empirically (LB) by comparison of the trifoliate leaf with a logarithmic scale of clover lamina area (Williams, Evans and Ludwig, 1964) prior to planimetric measurement of area (A) by the electronic planimeter.

To overcome the problem of partially defoliated leaflets, the scale was used to determine the potential area (i.e. all leaflets intact) which was then discounted by the amount of tissue missing on a proportion basis. The method of discounting is described in greater detail in section 3.2.6.2. The regression equation relating the two estimates of leaf area for clover is given below (equation 3.2.4.).

$$A = 0.07\ (\pm 1.81) + 0.90\ (\pm 0.02)\ LB, \qquad \ldots\ 3.2.4.$$

$$R^2 = 0.96^{***},\ n = 80.$$

3.2.5.6 Canopy Structure

Four 20cm x 20cm x 10cm samples of turf from each paddock were used to determine canopy structure. Ten tillers per grass species were selected by a vertical point first hit method and the height of the tips of all leaves and the ligule of the penultimate youngest leaf determined without disturbing the tiller. This was achieved using an inscribed dissection needle. The procedure was similar for clover stolons except that petiole height was determined. These measurements enabled tiller and leaf angles to be calculated and the relative position of a species in the canopy to be determined.

Plate 3.4 . A marked ryegrass tiller.

3.2.5.7 Lamina, Petiole, Pseudostem and Stolon Weight

The tillers and stolons measured in situ to determine canopy structure were removed from the sward after the measurements described in section 3.2.5.6 were completed. The length and mid-rib breadth of each lamina and the length of the residual preudostem was determined. The leaves for all ten tillers were then bulked on a leaf position basis and oven dried for 12 hours at 80°C and weighed. Pseudostem tissue was dried at the same time at the same temperature. The procedure used for clover was similar except that both petiole length and lamina area were determined. The procedure of discounting a potential area (section 3.2.5.5) was used.

3.2.6. FIELD TILLER/STOLON MEASUREMENTS

Measurements of lamina (petiole) length and pseudostem (stolon) length on individual tillers (stolons) were made on 5 successive occasions at 3-4 day intervals during each intensive measurement period. Forty tillers or stolons per species were marked in each paddock on day 1 with two transects per species, each of 5 units, located in each quarter of the paddock. Each transect was defined by two pegs and potential loci for marked units were at 10cm intervals. The procedure adopted during the marking process was to place a flat head nail with attached telephone wire in the ground (plate 3.4) at the appropriate 10cm interval mark and then select a tiller or stolon within range of the wire on a vertical first hit basis. If the tiller selected

Plate 3.5. A recording form for a ryegrass tiller.

PD	PLANT
1	3
2	1 1 4

S.N.	DATE	DYS		ST.	L.1 ST.1	L.2 ST.2	L.3 ST.3	L.4 ST.4	L.5 ST.5	SHEATH	REPROD.
6	8	14	16	17	19 22	24 27	29 32	34 37	39 42	44 47	49 52
1	20779				6 2 0	1 0 2 0	7 2 0	8 2 0	2 2 1 0	1 0	
2	50779				0	1 0	7	9	3 7 3 0	1 1	
3	90779				0	9	7	1 3 0	2 2 3 0	1 2	
3	90779		1		1 2 1 0						
4	120779				0	0	0 3 0	1	1 4 3 0	1 2	
4	120779		9		7 1 1						
4	120779		1		2 7 1 0						
5	160779				0	0	0	0	2 3 0	1 2	
5	160779		9		1 4 3 0						
5	160779		1		3 9						

A ' 9 ' in column 16 indicates that the record for the primary tiller is continued on this line. A ' 1 ' in column 16 indicates the presence of a daughter tiller with associated measurements on this line.

by this process was obviously an attached daughter tiller, it was rejected and a new tiller selected, but if a primary tiller with a daughter(s) was selected then the daughter tiller(s) was included in subsequent measurements as an integral part of the locus unit. In this manner 480 marked units were established.

If a plant unit was lost due to removal of the wire ring by treading or defoliation disturbance, it was replaced using the selection procedures outlined before.

3.2.6.1 Technique - Grasses

Both Lolium perenne L. and Poa annua L. were measured. The bottom-most leaf nearest the soil surface was identified as leaf 1. All the leaves above this and appearing subsequently were numbered in order of appearance, the youngest leaf having the highest number. This system was necessary to allow new leaves to be easily fitted into the recording procedure. A maximum sequence of 10 leaves could be measured in this way. The lengths of all laminae, the pseudostem from the ligule of the penultimate youngest leaf to ground level and the length of any reproductive stem, if present, from the flag leaf ligule to the seed head tip were measured. The laminae lengths of all daughter tillers were summed and entered as a single value attributable to daughter tillers, no attempt being made to measure the psuedostem length of these tillers. The total number of daughter tillers per locus was also recorded. A sample recording form is depicted in plate 3.5.

A simple series of codings was used to facilitate identification of particular leaves in the field and during subsequent analysis. At the initial measurement laminae were identified as either intact or having been defoliated some time earlier. The tips of defoliated leaves were slit with a dissection needle (2 - 5mm), and the slit if absent at a future measurement indicated that defoliation had occurred in the preceding interval. Defoliation of previously intact lamina was obvious. Only green lamina were measured. If a lamina had a dead tip, then the length measured was from the base of the lamina to the base of the dead tissue. If dead areas were irregular as in the case of fungal attack, then an estimate was made of the mean length of green tissue.

3.2.6.2 Technique - White Clover

While the same basic technique was employed to measure Trifolium repens L. as was used for the grasses (i.e. petioles = lamina and stolon = pseudostem), slightly different decision rules were used. If the petiole plus lamina unit was in any way defoliated, the proportion of lamina absent was recorded using a 0 - 9 scale. Reference to previous records with this information enabled recognition of subsequent defoliation. This 0 - 9 scale also enabled the potential lamina area per petiole calculated from the petiole length (section 3.2.8) to be discounted to the actual area of lamina present. As with the grasses the number of daughter stolon growing points per locus was recorded but only one, the

second back from the primary stolon growing point, was measured as a representative of them all. Petioles were measured individually as for terminal petioles and stolon length but whereas for primary stolon petioles a sequence of 10 could be measured, the maximum sequence of daughter petioles that could be measured was 5. In practice this limitation had little effect.

3.2.7. ANIMAL MEASUREMENTS

3.2.7.1 Liveweight

All ewes and lambs were weighed weekly (non-fasted) throughout the experiment using a portable weighing crate.

3.2.7.2 Herbage Intake

Herbage intake of both ewes and lambs was estimated using chromic oxide (Cr_2O_3) as the indigestible marker (Hodgson and Rodriguez, 1970). Six pairs of ewes and lambs from each treatment were dosed twice daily with 1g and 0.5g pellets respectively of paper impregnated with Cr_2O_3 (0.32 by dry weight) for 7 days prior to faecal sampling and for 5 days during sampling. Grab samples of faecal material were taken twice daily and the samples bulked on an individual animal basis for the 5 sample days. The faeces were dried, milled and samples taken for ashing and determination of Cr content. A modification of the technique

described by Williams, David and Iismaa (1962) utilising atomic absorption spectrophotometry was used for determination of Cr contents in the pellets and faeces.

The digestibility of the ingested herbage was determined from *in vitro* analyses of material collected by the oesophageal fistulate ewes using the method described by Alexander and McGowan (1966). Four oesophageal fistulate ewes were rotated around the four treatments during each intensive measurement period, one per treatment, using a latin square design to enable systematic between-animal variation to be accounted for. The animals were penned for approximately two hours prior to sample collection. The samples collected were divided, one half for *in vitro* digestibility analysis and the other for subsequent botanical separation (section 3.2.7.3). Both were frozen and the sample for digestibility determination freeze dried and milled prior to analysis.

3.2.7.3. Botanical Composition of the Ewe's Diet

The composition of the diet was determined by separating extrusa samples into the following components : live and dead grass lamina, live and dead pseudostem, live and dead reproductive grass stem, grass seed head, live and dead clover lamina, live and dead clover petiole, clover stolon, weed, moss, roots, and remainder. The latter category was especially necessary on the 500 kg OM ha^{-1} treatment where particles of soil were present

Plate 3.6. A bitemeter attached to a Greyface ewe on the 1000 sward.

in the diet. The samples were analysed in petri dishes illuminated from beneath by a light source. Separated components were oven dried at 80°C for 24 hours prior to weighing.

3.2.7.4 Grazing Behaviour

Bite meters (Chambers, Hodgson and Milne, 1981) were used to record the total number of bites per day and the total grazing time (plate 3.6). The sensing devices were attached to a head harness and the main instrument to a body harness. Measured values were recorded each morning.

The meters (2 per paddock) were rotated every two days around the ewes used to determine herbage intake and in this way between 6 and 14 complete grazing day records per treatment per period were obtained. Equipment failure was the main reason for the variable number of records.

Mean intake per bite was determined by dividing mean herbage intake per day (g OM ewe^{-1} day^{-1}) by the total number of recorded bites per day.

3.2.8. DATA HANDLING - FIELD INDIVIDUAL UNIT DATA

A series of 'Fortran IV' routines was written for use on an ICL 2980 computer to manipulate raw field data into a form acceptable for statistical analysis by packages such as 'Genstat'.

Prior to the manipulation of the data by these routines, all the data were manually checked for obvious errors which were corrected. Details of the routines are given in appendices 1 and 2.

The philosophy behind the development of the routines was to provide a general purpose data base which could be used as the input for routines examining particular aspects of the data. After some initial data standardisation procedures (Appendix 1), the field grass lamina length values were multiplied by a mean mid-rib breadth value (section 3.2.5.7) to obtain an area per lamina which was corrected by a regression equation relating planimetric determined leaf area to length x breadth estimated area (section 3.2.5.5). The procedure for white clover was more complex and involved the use of a regression equation relating the potential area (all leaflets intact) of a trifoliate leaf to the length of petiole supporting it. The proportion of lamina missing (recorded in the field) was subtracted from the potential area to give the actual area of clover lamina present. Potential (PA) clover lamina area (all three leaflets intact) was related to petiole length (P) supporting the lamina by equation 3.2.5.

$$PA = 4.87\ (\pm 1.13)\ P^{0.94(\pm 0.05)} \qquad \ldots\ 3.2.5.$$

$$R^2 = 0.69^{***},\ n = 165.$$

This power law model, although not significantly different to a linear model, was preferred because it accounted for 0.033 more of the total variation. Petiole length varied between 2 and 70mm.

Mean lamina weight per unit area, mean pseudostem, mean petiole, mean stolon and mean reproductive stem weights per unit length (section 3.2.5.7) were used to convert area and length data into weights.

The mean mid-rib breadth and weight per unit area values of the youngest leaf on primary tillers were used for daughter tiller lamina length conversions. The values used for all lamina except the youngest and daughter tiller leaves were the means for all the other live leaves. No distinctions were made between young and old lamina tissue for white clover.

Differences in length, area, or weight between successive measurements for individual laminae and pseudostems etc. were calculated and if a tiller (stolon) had not been grazed during the period under review, then all the differences indicating growth were summed to provide an estimate of tiller (stolon) growth and all the differences indicating senescence summed to provide an estimate of tiller (stolon) senescence. The net production of the tiller (stolon) for the interval was calculated by subtracting the senescence term from the growth term. If, however, a tiller (stolon) was defoliated during the interval, then provided that there had been a non-defoliation interval prior to the current interval, the growth or senescence rate of the defoliated lamina in the previous interval was inspected to obtain an estimate of the growth or senescence that would have occurred had the lamina not been defoliated. This model was preferred to that of obtaining a mean growth or senescence rate for all undefoliated lamina of similar rank over the same interval because it was

considered that mean values did not adequately reflect differences in tiller size, stage of growth etc.. If no estimate of growth or senescence could be obtained because for example, the tiller (stolon) had been defoliated in the previous interval also, then zero values were assumed.

Mean 'per day' values for each successive interval between measurements were themselves meaned to give overall period 'per day' values which were then statistically analysed.

Species performance on a per unit area basis (kg OM ha^{-1} day^{-1}) was obtained by multiplying mean locus values by a constant derived from the population density of the species (units m^{-2}) divided by the number of units per locus. Leaf area index (LAI) values were calculated in a similar manner.

The amount of tissue removed by defoliation was calculated by adding an estimate of the growth or senescence that would have occurred had defoliation not taken place to the measured loss of tissue. Consumption per species per defoliation per unit area (kg DM ha^{-1}) was obtained by multiplying the amount of tissue removed per tiller (stolon) by a constant as for species performance (see previous paragraph). Consumption rate per unit area (kg DM ha^{-1} day^{-1}) was obtained by dividing consumption per defoliation by the mean interval between defoliations which was calculated by the method advocated by Fenlon (1978). This method uses the geometric distribution rather than the binomial distribution as used by Hodgson (1966) and has the advantage that marked plants

TABLE 3.2.9.1. ANALYSIS OF VARIANCE

VARIATE: TOTAL GROWTH PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	82.1	0.01	82.1	0.105
TRANSECT. TILLERS STRATUM	8	5492.4	0.36	686.6	0.874
TRANSECT. TILLERS. UNITS STRATUM					
TIME	1	57.0	0.00	57.0	0.073
SPECIES	2	421922.9	27.84	210961.4	268.615
PADDOCKS	3	105478.7	6.96	35159.6	44.768
QUARTERS	3	20591.1	1.36	6863.7	8.740
TIME. SPECIES	2	6859.1	0.45	3429.5	4.367
TIME. PADDOCKS	3	1958.5	0.13	652.8	0.831
SPECIES. PADDOCKS	6	144573.4	9.54	24095.6	30.681
TIME. QUARTERS	3	7784.2	0.51	2594.7	3.304
SPECIES. QUARTERS	6	14891.0	0.98	2481.8	3.160
PADDOCKS. QUARTERS	9	5119.8	0.34	568.9	0.724
TIME. SPECIES. PADDOCKS	6	49259.7	3.25	8209.9	10.454
TIME. SPECIES. QUARTERS	6	20208.1	1.33	3368.0	4.288
TIME. PADDOCKS. QUARTERS	9	18478.2	1.22	2053.1	2.614
SPECIES. PADDOCKS. QUARTERS	18	10531.1	0.69	585.1	0.745
RESIDUAL	869 (4)	682482.9	45.04	785.4	
TOTAL	946	1510195.0	99.66	1596.4	
GRAND TOTAL	955	1515769.0	100.03		

ESTIMATED GRAND MEAN	25.79
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

need only be observed up to the first defoliation. Fenlon (pers. comm.) contends that not only is the method more flexible but the assumptions implicit in it are more plausible than those in the binomial model.

3.2.9. STATISTICAL ANALYSIS

Two statistical packages mounted on the Edinburgh Regional Computing Centre ICL 2980 computer, 'Genstat' and 'Multreg' were used to analyse the data. Genstat was used for all the analyses of variance and for parameter estimation for non-linear models. Multreg was used solely for regression analyses.

A major problem associated with individual plant data is that the distributions of the data are often skewed and the presence of negative values, which are an integral part of the data, makes transformation of the data difficult. An equally serious problem is that measurement of only 480 individual plant units twice a week requires considerable labour resource and consequently land replication of treatments was not possible.

The data for all three species for both periods were combined untransformed into a single analysis of variance for each variable. A sample analysis of variance (ANOVA) table which is representative of all individual plant unit analyses is given in table 3.2.9.1. The layout of the individual plant units in transects and quarters (section 3.2.6) is reflected in the table,

and the use of transects and quarters was intended as a means of identifying variance within the treatment paddocks. Herbage production varied between paddock quarters as is evident from the significant quarter effect.

The species and paddocks (treatments) main effect terms were invariably highly significant but so too were the species x paddocks and time (period) x species x paddocks interaction terms. Therefore, the main effect terms are of limited value with regard to interpretation of the results and they have only been used to indicate the magnitude and order of differences between species. The time x species x paddocks interaction term has been extracted from all the ANOVA tables and an inflated least significant difference test (LSD 5%) used to compare between treatments and periods within species. The LSD value used was that appropriate for making comparisons between any pair of values within the interaction table (i.e. across species as well as treatments and periods). It was considered that comparing treatment and period effects within a species using an inflated LSD value would help to prevent attributing significance to differences that may have occurred due to irregularity in variance estimates due to skewness. Also, the impact of the very high number of degrees of freedom associated with the residual term means that significance can be achieved with relatively small variance ratios, and therefore some caution should be exercised.

Wherever possible the analyses of variance have been regarded as the preliminary analysis and have been followed by regression analysis with actual rather than treatment identifier herbage mass levels as the independent variate in attempts to define the patterns of response. With few exceptions, the data from both periods have been combined to obtain an overall response and it is recognised that if period x treatment interactions are significant, such analyses ignore this interaction. However, with only 8 data points from the two periods combined, there was no alternative and wherever an interaction is clearly present in the data, it is recognised and discussed.

The regression models fitted included linear, quadratic, rectangular hyperbola and logistic functions. Wherever two or more models have been fitted to the same set of data, both R^2 and RMS (residual mean square) data are provided. If only one model has been fitted then only the R^2 value is given.

The herbage intake, diet botanical composition and grazing behaviour data were analysed using standard ANOVA techniques on a within period basis initially and the periods combined for regression analyses if it seemed appropriate.

Table 3.3.2.1 Mean sward surface height (cm) and mean herbage mass (kg OM ha^{-1}) for both periods.

	Herbage Height		Herbage Mass †	
Treatment	Period 1	Period 2	Period 1	Period 2
500	1.32 ± 0.08	1.16 ± 0.07	528	474
700	1.87 ± 0.10	1.82 ± 0.09	704	689
1000	2.95 ± 0.15	3.04 ± 0.16	1018	1043
1700	7.22 ± 0.41	5.91 ± 0.39	1829	1654

† A mean value for the period calculated from equation 3.2.1.

3.3. R E S U L T S

3.3.1. INTRODUCTION

The actual levels of herbage mass achieved rather than the proposed levels (section 3.2.2.) will henceforth be used to describe the treatments. Thus the treatment swards of mean herbage mass 500, 700, 1000 and 1700 kg OM ha^{-1} will be referred to as the 500 sward etc.. Where appropriate, in all figures, data from period 1 will be distinguishable from that of period 2 as follows: period 1 data closed symbols (e.g. •), period 2 open symbols (e.g. o).

3.3.2. HERBAGE MASS AND HERBAGE WEIGHT

Sward mass was estimated from mean sward height for the period using equation 3.2.1.

The only sward to vary markedly in both height and mass between the two periods was the 1700 sward (table 3.3.2.1.), the remainder of the treatment swards showed little variation between the two periods.

The stocking rates (ewes + single lambs) required to achieve the herbage mass and height values detailed in table 3.3.2.1. are depicted in figure 3.3.7.1.

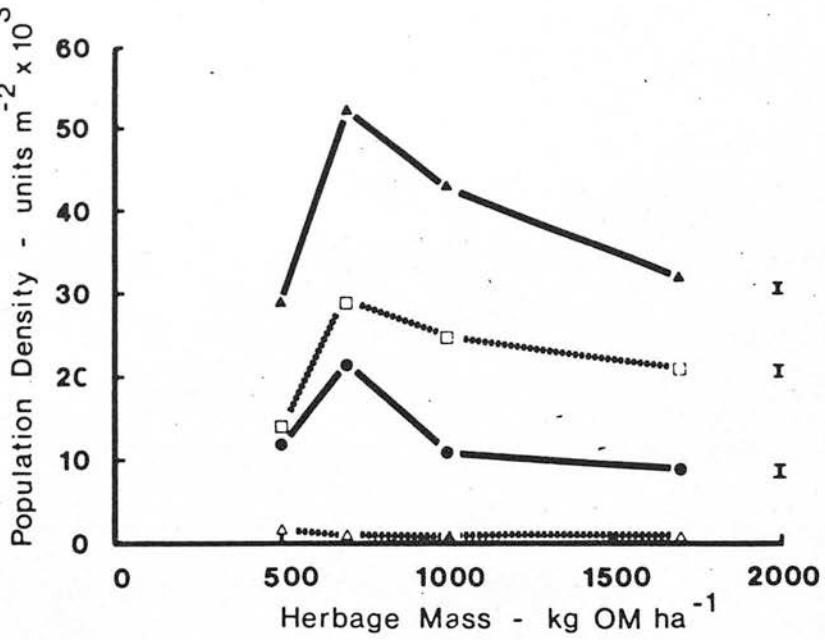

Figure 3.3.3.1 Total (▲—▲), ryegrass (□···□), Poa annua (●—●) and clover (△···△) population densities. (Means of both periods).

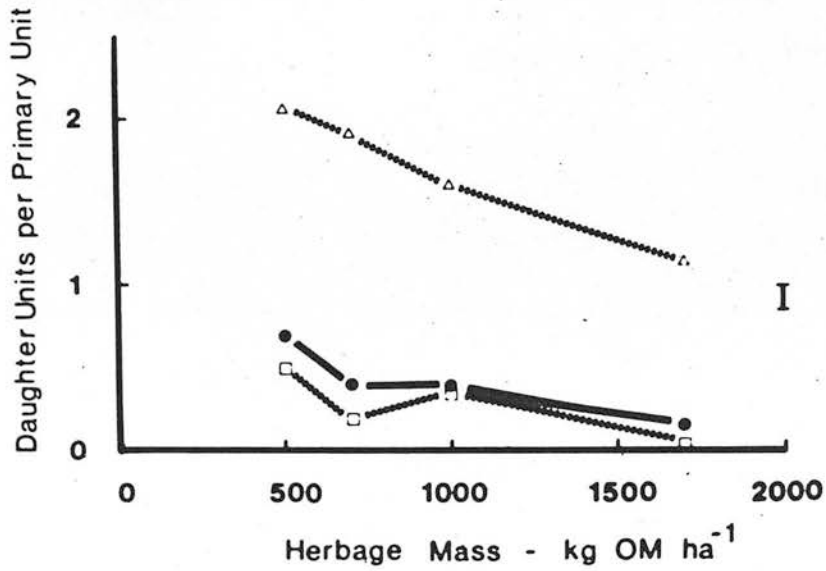

Figure 3.3.4.1 Number of clover (△···△), Poa annua (●—●) and ryegrass (□···□) daughter units per primary unit. (Means of both periods).

3.3.3. SPECIES POPULATION DENSITY

Mean species and total population densities for the two periods are depicted in figure 3.3.3.1. More detail is given in table 1 of appendix 3.

The total, ryegrass and Poa population densities were lowest in the 500 treatment, rose rapidly to be highest in the 700 treatment and then fell gradually in the 1000 and 1700 treatments. There were no significant differences in clover stolon growing point densities between the four treatments.

3.3.4. DAUGHTER TILLER (STOLON) NUMBER

Daughter tiller or stolon numbers per primary unit (section 3.3.5) were highest in the 500 and lowest in the 1700 treatment (figure 3.3.4.1). The numbers of daughter tillers per primary tiller for Poa were slightly but not significantly higher than for ryegrass. Daughter stolon numbers per primary stolon were much higher than grass daughter tillers numbers and decreased as herbage mass increased. More detail is given in table 2 of appendix 3.

3.3.5. SPECIES PERFORMANCE

A primary tiller or stolon refers to the main tiller or main stolon terminal growing point only, and not to daughter tiller or stolon tissue. Lamina growth, pseudostem (stolon) growth, total growth (lamina + pseudostem (stolon) + reproductive stem), lamina senescence and net production (total growth - senescence) rates per primary tiller or stolon (μg DM tiller (stolon)$^{-1}$ day^{-1})

Table 3.3.5.1. Leaf area per primary tiller (stolon) in mm^2.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	41 d[1/]	52 de	42 d
	700	47 d	47 e	36 d
	1000	83 c	78 c	76 c
	1700	168 a	156 a	131 a
2	500	39 d	50 de	36 d
	700	37 d	36 e	40 d
	1000	70 c	69 cd	69 c
	1700	121 b	111 b	110 b
		SE[2/] = 7.6	LSD = 21.7	

Table 3.3.5.2. Leaf area index (LAI)

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	0.49 e	0.46 b	0.04 a
	700	0.84 d	1.07 a	0.02 a
	1000	1.77 b	0.39 b	0.04 a
	1700	3.98 a	0.89 a	0.07 a
2	500	0.38 e	0.39 b	0.02 a
	700	1.28 c	0.46 b	0.02 a
	1000	1.49 c	0.86 a	0.02 a
	1700	1.97 b	1.09 a	0.07 a
		SE = 0.10	LSD = 0.28	

1/ Values in columns without common lower case letters are significantly ($P < 0.05$) different.

2/ In this and subsequent tables 'SE' is the standard error of the mean.

and per unit area (kg DM ha^{-1} day^{-1}) are detailed. For white clover lamina includes petiole tissue.

Analysis of variance tables are given in appendix 4.

3.3.5.1. Leaf Area per Primary Tiller (Stolon) and Leaf Area Index

For all three species, leaf area per primary tiller (stolon) increased with herbage mass (table 3.3.5.1.) and with the exception of the 1700 treatment in period 1, there were no significant differences between species.

Overall, ryegrass leaf area index was significantly greater ($P < 0.05$) than that for Poa which in turn was significantly greater than that for white clover (1.53 vs 0.70 vs 0.04 $\pm$ 0.03). Leaf area index for ryegrass in both periods and Poa in period 2 increased with herbage mass (table 3.3.5.2.). Leaf area index for white clover was highest in the 1700 treatment.

3.3.5.2 Species Primary Tiller (Stolon) Performance

Lamina, pseudostem (stolon) and total growth rates per primary tiller or stolon were highest in white clover followed by ryegrass and then Poa (table 3.3.5.3). Lamina senescence rates per primary tiller or stolon were similar in ryegrass and Poa, higher than the rate for white clover.

Table 3.3.5.3. Main effect species primary tiller (stolon) performance in μg DM tiller (stolon)$^{-1}$ day^{-1}.

	Ryegrass	Poa annua	White clover	SE
Lamina growth	178 b[1/]	73 c	360 a	8.4
Pseudostem (stolon) growth	71 b	48 c	94 a	8.0
Total growth	258 b	162 c	454 a	12.9
Senescence	90 a	84 a	58 b	6.3

1/ Values in rows without common lower case letters are significantly ($P < 0.05$) different.

Table 3.3.5.4. Lamina growth on primary tillers and stolons in μg DM tiller (stolon)$^{-1}$ day^{-1} .

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	148 bc	9 b	279 c
	700	144 bc	79 a	256 c
	1000	283 a	104 a	459 b
	1700	298 a	41 ab	681 a
2	500	102 c	70 ab	228 c
	700	109 c	81 a	265 c
	1000	139 bc	107 a	284 c
	1700	198 b	91 a	432 b
		SE = 23.8	LSD = 68.1	

Table 3.3.5.5. Pseudostem and stolon growth on primary tillers and stolons in μg DM tiller (stolon)$^{-1}$ day^{-1}.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	14 d	1 b	50 cd
	700	27 cd	27 b	62 cd
	1000	52 cd	74 a	169 ab
	1700	84 bc	49 ab	213 a
2	500	1 d	49 ab	35 d
	700	22 cd	35 ab	51 cd
	1000	248 a	75 a	54 cd
	1700	118 b	73 a	115 bc
		SE = 22.6	LSD = 64.5	

1) For tables 3.3.5.4. - 3.3.5.7. values in columns without common lower case letters are significantly ($P < 0.05$) different.
2) Whenever LSD (least significant difference) values are given, they can be used to compare any pair of values in the table at the $P < 0.05$ significance level.

Lamina growth rates per primary tiller or stolon for ryegrass and white clover generally increased with herbage mass (table 3.3.5.4). Lamina growth rates for Poa primary tillers were highest in the 1000 and least in the 500 treatment in both periods.

Ryegrass pseudostem in period 1 and clover stolon growth rates in both periods increased with herbage mass (table 3.3.5.5.). In both periods for Poa and period 2 for ryegrass, pseudostem growth rates were highest in the 1000 treatment.

Total growth rates per tiller or stolon responded to treatment in a manner similar to lamina growth with the exception of ryegrass total growth rate which was highest in the 1000 rather than the 1700 treatment in period 2 (table 3.3.5.6.).

Table 3.3.5.6. Total growth on primary tillers and stolons in μg DM tiller (stolon)$^{-1}$ day^{-1}.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	162 b	11 e	329 c
	700	171 b	154 bcd	318 c
	1000	335 a	259 a	628 b
	1700	382 a	90 de	894 a
2	500	102 b	136 cd	262 c
	700	131 b	136 cd	316 c
	1000	401 a	217 abc	338 c
	1700	382 a	255 ab	547 b

SE = 36.4 LSD = 104.1

However, whereas overall ryegrass lamina growth rate was significantly ($P<0.05$) greater in period 1 than period 2 (219 vs 137 $\pm$ 11.9 µg DM day^{-1}), total growth rate was not significantly different (263 vs 254 $\pm$ 18.2 µg DM day^{-1}). Neither Poa lamina growth nor total growth rates differed significantly between periods but both clover lamina and total growth rates were significantly ($P<0.05$) higher in period 1 than period 2 (419 vs 302 $\pm$ 11.9; 542 vs 366 $\pm$ 18.2 µg DM day^{-1}).

Lamina senescence rates per primary tiller or stolon were similar in the two grasses and greater than that in white clover (table 3.3.5.7). Lamina senescence rates per primary tiller or stolon tended to increase with herbage mass.

Net production rates for primary tillers and stolons are given in table 3 of appendix 3.

Table 3.3.5.7. Lamina senescence on primary tillers and stolons in µg DM tiller (stolon)$^{-1}$ day^{-1}.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	77 bc	9 d	15 b
	700	80 bc	126 ab	32 b
	1000	93 bc	104 abc	23 b
	1700	170 a	54 cd	208 a
2	500	43 cd	74 c	28 b
	700	40 d	79 bc	54 b
	1000	81 bc	84 bc	37 b
	1700	127 b	147 a	63 b

SE = 17.9 LSD = 51.1

Table 3.3.5.8. Main effect species per unit area performance in kg DM ha^{-1} day^{-1}.

	Ryegrass	Poa annua	White clover	SE
Lamina growth	38.8 a[1/]	11.6 b	3.0 c	0.98
Pseudostem (stolon) growth	13.4 a	4.4 b	0.4 c	1.02
Total growth	53.9 a	20.1 b	3.5 c	1.57
Senescence	17.2 a	9.4 b	0.4 c	0.95
Net production	36.6 a	10.7 b	3.1 c	1.70

1/ Values in rows without common lower case letters are significantly ($P < 0.05$) different.

3.3.5.3. Species per unit area performance

Lamina growth, pseudostem (stolon) growth, total growth, lamina senescence and net production rates per hectare were highest for ryegrass followed by Poa and then white clover (table 3.3.5.8). The contributions of white clover were small.

Ryegrass lamina growth rate increased with herbage mass in period 1 but not in period 2 (table 3.3.5.9.) and over all treatments, was significantly ($P < 0.01$) higher in period 1 than in period 2 (47.9 vs 29.8 $\pm$1.4 kg DM $ha^{-1}day^{-1}$). Over all treatments, Poa lamina growth rate was higher in period 2 than period 1 (13.4 vs 9.8 $\pm$1.40 kg DM ha^{-1} day^{-1}) and the highest

Table 3.3.5.9 Lamina growth per unit area in kg DM $ha^{-1}day^{-1}$.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	20.9 d[1/]	0.9 e	4.1 a
	700	28.9 c	26.1 a	2.6 a
	1000	67.7 a	9.5 bcd	3.5 a
	1700	73.8 a	2.6 de	4.3 a
2	500	11.7 e	8.3 cde	2.8 a
	700	39.1 b	12.1 bc	2.0 a
	1000	34.0 bc	16.2 bc	0.9 a
	1700	34.6 bc	16.8 b	3.7 a
		SE = 2.8	LSD = 8.0	

1/ For tables 3.3.5.9.- 3.3.5.13. values in columns without common lower case letters are significantly ($P < 0.05$) different.

Table 3.3.5.10. Pseudostem and stolon growth per unit area in kg DM ha^{-1} day^{-1}.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	1.5 e	0.1 b	0.3 a
	700	4.6 de	6.0 ab	0.3 a
	1000	10.2 cd	3.2 ab	0.7 a
	1700	20.4 b	2.9 ab	1.1 a
2	500	0.1 e	3.4 ab	0.1 a
	700	7.1 de	3.4 ab	0.3 a
	1000	45.3 a	9.0 a	0.1 a
	1700	18.4 bc	7.5 ab	0.6 a
		SE = 2.9	LSD = 8.3	

Table 3.3.5.11. Total growth per unit in kg DM $ha^{-1}day^{-1}$.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	22.4 ef	1.1 e	4.4 a
	700	33.5 e	42.4 a	3.0 a
	1000	77.9 b	18.1 cd	4.3 a
	1700	94.3 a	5.5 de	5.5 a
2	500	11.8 f	13.1 de	3.0 a
	700	46.2 d	17.9 cd	2.3 a
	1000	81.5 b	29.0 bc	1.0 a
	1700	63.3 c	33.4 ab	4.2 a
		SE = 4.4	LSD = 12.7	

lamina growth rate for Poa was achieved in the 700 treatment in period 1. Clover lamina growth rates were not significantly influenced by herbage mass.

Ryegrass pseudostem growth rate increased with herbage mass in period 1 but not in period 2 (table 3.3.5.10) and over all treatments was significantly ($P < 0.01$) higher in period 2 than period 1 (17.7 vs 9.2 $\pm$1.45 kg DM ha^{-1} day^{-1}). Poa pseudostem and white clover stolon growth rates were not significantly affected by herbage mass in either period and were generally lower than those for ryegrass.

Ryegrass total growth rate in period 1 and Poa total growth rates in period 2 increased with herbage mass (table 3.3.5.11). In period 2 ryegrass total growth rate was highest in the 1000 treatment and Poa total growth rate in period 1 was highest in the 700 treatment. The total growth rate of white clover was not significantly affected by herbage mass. Over all treatments, the total growth rate of ryegrass was significantly ($P < 0.05$) higher in period 1 than period 2 (57.0 vs 50.7 $\pm$2.22 kg DM $ha^{-1}day^{-1}$) whereas the reverse ($P < 0.05$) was the case for Poa (16.8 vs 23.4 $\pm$2.22 kg DM ha^{-1} day^{-1}).

Table 3.3.5.12 Lamina senescence per unit area in kg DM ha^{-1} day^{-1}.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	8.3 cd	0.7 d	0.2 a
	700	13.6 bc	27.0 a	0.3 a
	1000	18.9 b	4.7 cd	0.1 a
	1700	43.0 a	3.1 cd	1.2 a
2	500	4.0 d	6.3 cd	0.2 a
	700	14.4 bc	8.8 bc	0.3 a
	1000	15.5 bc	10.2 bc	0.1 a
	1700	20.2 b	14.0 b	0.5 a
		SE = 2.7	LSD = 7.6	

Table 3.3.5.13 Net production per unit area in kg DM ha^{-1} day^{-1}.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	14.1 f	0.4 c	4.2 a
	700	20.0 ef	15.4 ab	2.7 a
	1000	59.0 ab	13.5 abc	4.2 a
	1700	51.3 bc	2.4 bc	4.3 a
2	500	7.8 f	6.8 abc	2.8 a
	700	31.8 de	9.0 abc	2.0 a
	1000	66.0 a	18.8 a	0.9 a
	1700	43.1 cd	19.4 a	3.8 a
		SE = 4.8	LSD = 13.8	

Lamina senescence rates for ryegrass in both periods and Poa in period 2 increased with herbage mass (table 3.3.5.12). In period 1, the highest lamina senescence rate for Poa occurred in the 700 treatment. Lamina senescence rates in white clover were unaffected by herbage mass. Over all treatments, lamina senescence rates for ryegrass were significantly ($P < 0.01$) higher in period 1 than period 2 (20.9 vs 13.5 $\pm$ 1.34 kg DM ha^{-1} day^{-1}) whereas lamina senescence rates for both Poa and white clover were not significantly different between periods.

Net production rates for ryegrass increased with herbage mass to a maximum in the 1000 treatment and then declined in both periods (table 3.3.5.13). In period 2, Poa net production rate increased with herbage mass. White clover net production rates were not affected by treatment. Over all treatments Poa net production rate was significantly ($P < 0.05$) greater in period 2 than period 1 (13.5 vs 7.9 $\pm$ 2.41 kg DM ha^{-1} day^{-1}) but there was no significant difference for ryegrass (37.2 vs 36.1 $\pm$ 2.41 kg DM ha^{-1} day^{-1}).

3.3.5.3. Combined Species (Sward) Per Unit Area Performance

Lamina growth (G_L), total growth (G_T), lamina senescence (S_L) and net production (NP) data for the three species were combined to obtain overall sward estimates of these parameters.

Three models, rectangular hyperbola (equation 3.3.5.1), piece-wise linear (equation 3.3.5.2) and logistic (equation 3.3.5.3)

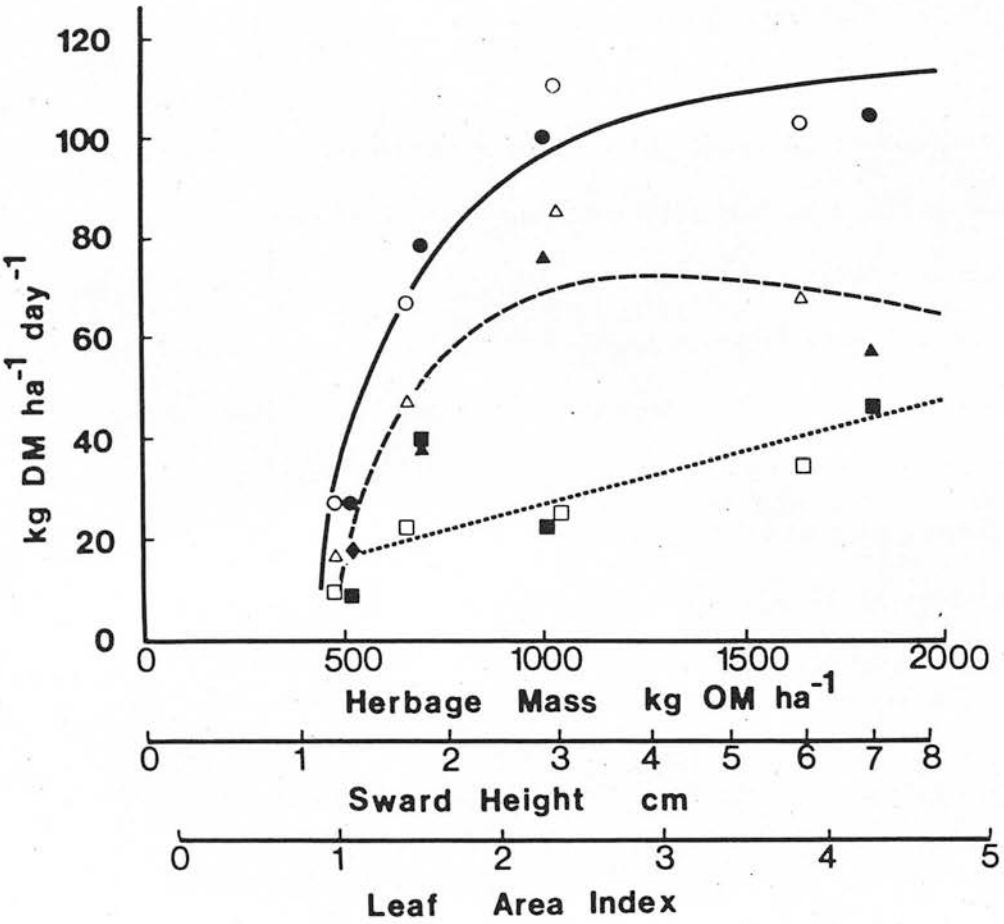

Figure 3.3.5.1 The relationships between total growth (●—○), senescence (■···□) and net production (▲---△); and herbage mass, herbage height and LAI using the rectangular hyperbola model for total growth.

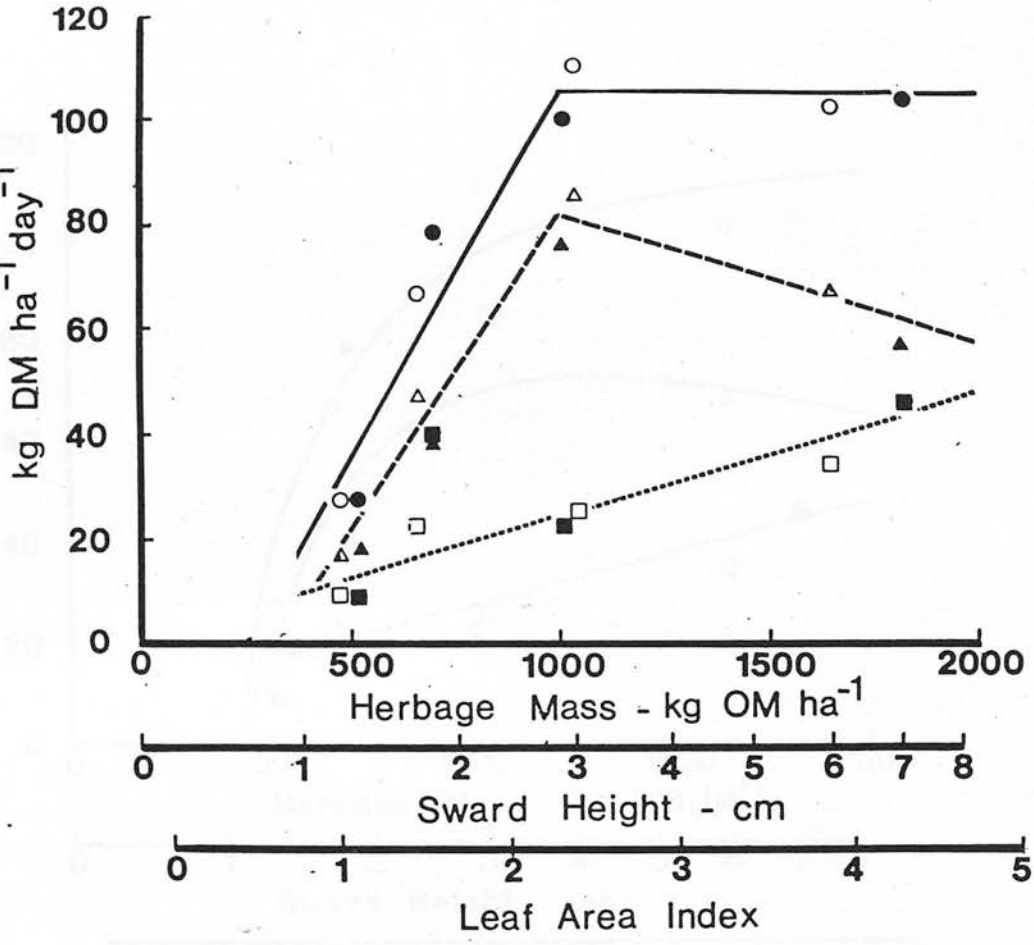

Figure 3.3.5.2 The relationships between total growth (●—○), senescence (■···□) and net production (▲---△); and herbage mass, herbage height and LAI using the piece-wise linear model for total growth.

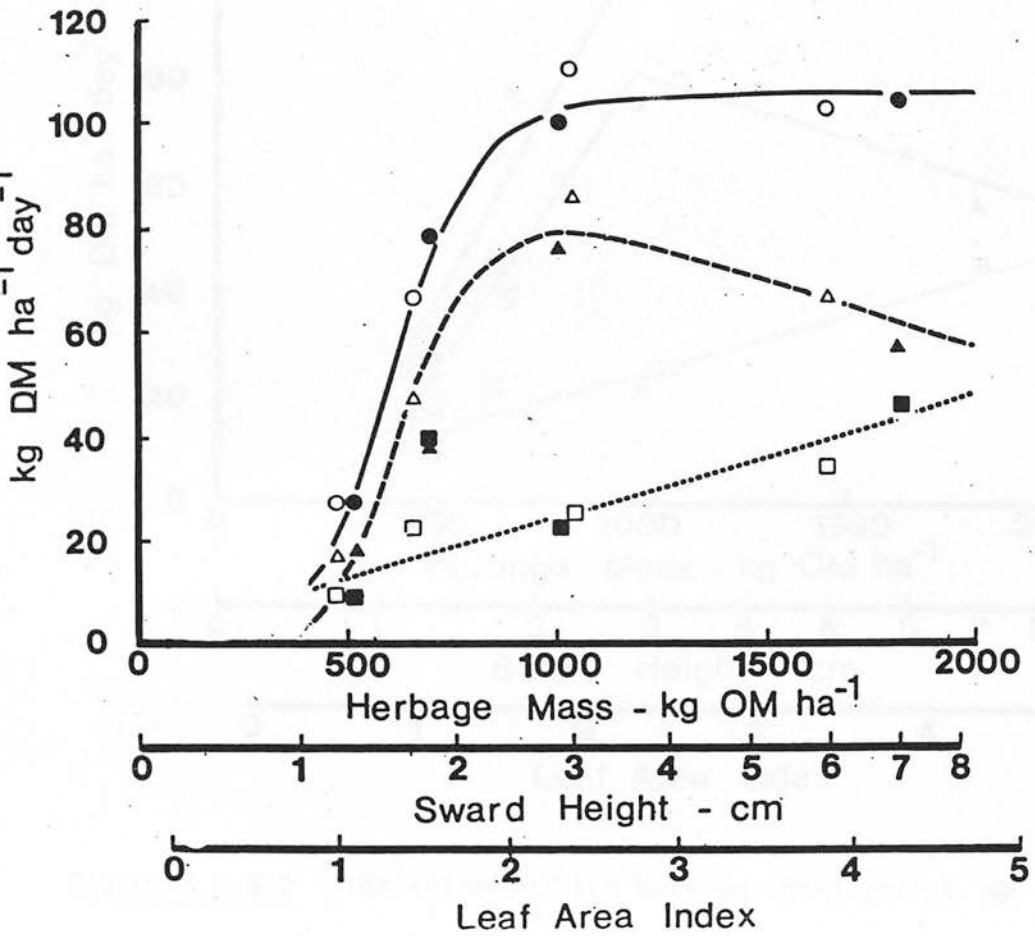

Figure 3.3.5.3 The relationships between total growth (●—○), senescence (■···□) and net production (▲---△); and herbage mass, herbage height and LAI work using the logistic model for total growth.

were fitted to the total growth data from both periods using herbage mass (HM) as the independent variate.

$$G_T = 117.7 \ (\pm 5.4) - \frac{2.174948 \times 10^7 \ (\pm 2.313 \times 10^6)}{HM^2} \quad \ldots 3.3.5.1$$

$R^2 = 0.94^{***}$, RMS = 86.31, n = 8.

$$G_T = \begin{cases} 106.1 & HM > 1004 \\ -35.6 \ (\pm 15.4) + 0.14 \ (\pm 0.02) \ HM, & HM \geqslant 258 \quad HM \leqslant 1004 \\ 0 & HM < 258 \end{cases}$$

$R^2 = 0.94^{***}$, RMS = 77.28, n = 8. ... 3.3.5.2

$$G_T = \frac{106.1 \ (\pm 3.1)}{(1 + 337.8 \ (\pm 287.6) \ e} - 0.0095 \ (\pm 0.0014) \ HM$$

$R^2 = 0.98^{***}$, RMS = 32.46, n = 8. ... 3.3.5.3

A linear model for lamina senescence including all the data (equation 3.3.5.4) accounted for considerably less of the total variation (0.56 vs 0.91) than the same model when the data for the 700 treatment in period 1 was omitted (equation 3.3.5.5).

$$S_L = 7.2 \ (\pm 7.9) + 0.019 \ (\pm 0.007) \ HM \quad \ldots 3.3.5.4$$

$R^2 = 0.56^{*}$, RMS = 92.94, n = 8.

$$S_L = 0.45 \ (\pm 3.77) + 0.023 \ (\pm 0.003) \ HM \quad \ldots 3.3.5.5$$

$R^2 = 0.91^{***}$, RMS = 18.44, n = 7.

Table 3.3.5.14 Overall and period lamina growth rate (G_L) versus herbage mass (HM).

1. Rectangular hyperbola model

Overall: $G_L = 75.5\ (\pm 7.03) - \dfrac{1.200189 \times 10^7\ (\pm 3.0249 \times 10^6)}{HM^2}$

$R^2 = 0.72^{**}$, RMS = 147.59, n = 8.

Period 1: $G_L = 91.8\ (\pm 5.31) - \dfrac{1.775048 \times 10^7\ (\pm 2.5065 \times 10^6)}{HM^2}$

$R^2 = 0.96^{*}$, RMS = 38.72, n = 4.

Period 2: $G_L = 60.8\ (\pm 5.75) - \dfrac{7.7705 \times 10^6\ (+2.2893 \times 10^6)}{HM^2}$

$R^2 = 0.85^{P = 0.08}$, RMS = 51.63, n = 4.

2. Logistic model

Overall: $G_L = \dfrac{67.22\ (\pm 6.46)}{(1 + 352.1\ (^{+}-1028.7)\ e} - 0.0106\ (\pm 0.0053)\ HM$

$R^2 = 0.75^{**}$, RMS = 158.47, n = 8.

Period 1: $G_L = \dfrac{81.43\ (\pm 0.94)}{(1 + 328.7\ (\pm 113.5)\ e} - 0.0095\ (\pm 0.0006)\ HM$

$R^2 = 0.999^{**}$, RMS = 1.4799, n = 4.

Period 2: Model could not be fitted.

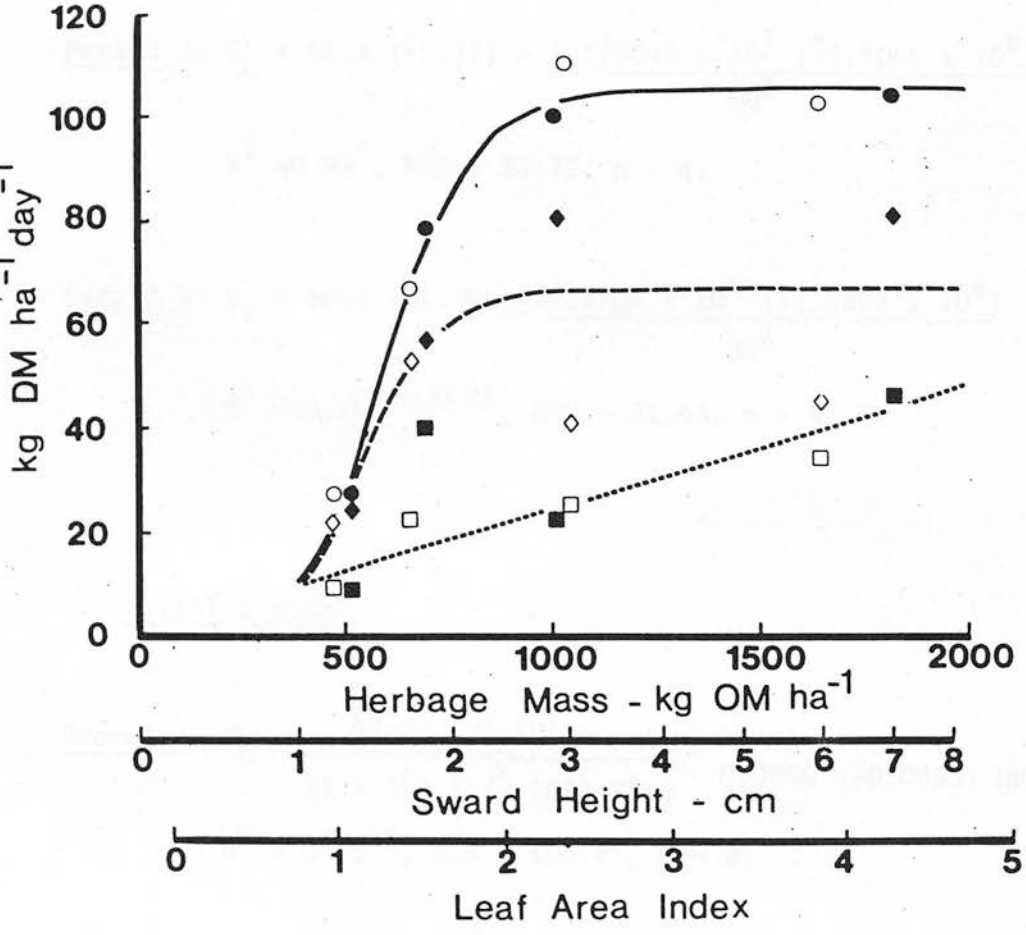

Figure 3.3.5.4 The relationships between total growth (●—○), lamina growth (◆---◇) and senescence (■···□); and herbage mass, herbage height and LAI using logistic models for both total and lamina growth.

The relationships of total growth, as represented by rectangular hyperbola, piece-wise linear and logistic models, lamina senescence as represented by equation 3.3.5.5 and net production (the difference between the total growth and lamina senescence functions) are depicted in figures 3.3.5.1, 3.3.5.2 and 3.3.5.3. The sward height and leaf area index scales were derived from regression equations using these parameters as the dependent variates and herbage mass as the independent variate (table 4 of appendix 3).

Rectangular hyperbola and logistic models were fitted to the overall and individual period lamina growth rate data (table 3.3.5.14). Individual period models were fitted because inspection of the data indicated that the lamina growth rates in period 1 were higher than those in period 2 for the 1000 and 1700 treatments. Overall and for period 1, the logistic models accounted for slightly, but not significantly, more of the total variation than the rectangular hyperbola models. The overall logistic model for lamina growth is depicted in figure 3.3.5.4.

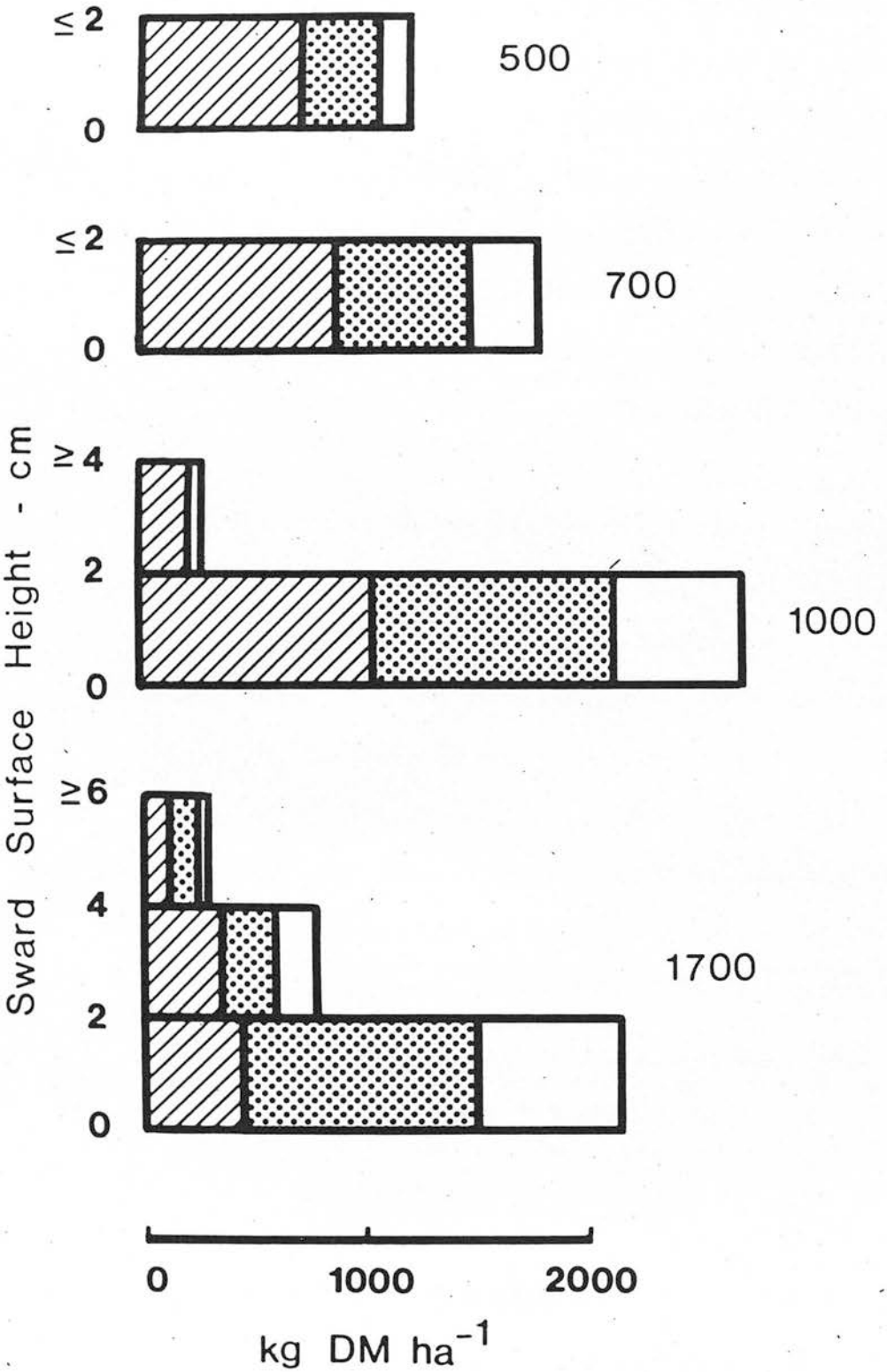

Figure 3.3.6.1 Distribution of green lamina , green stem and dead tissue in the sward canopy in period 2.

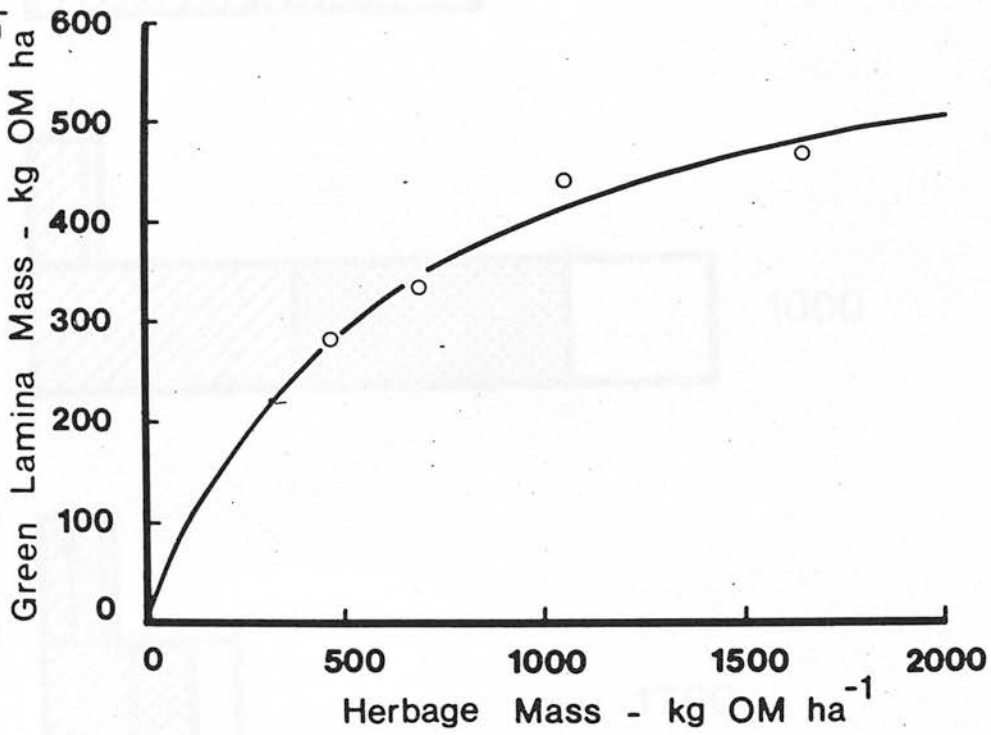

Figure 3.3.6.2 The relationship between green lamina mass and herbage mass in period 2.

3.3.6. SWARD STRUCTURE

Two measures of sward structure, canopy structure and canopy geometry (Thomas, 1980) are detailed in this section.

3.3.6.1 Canopy Structure

The distribution of the components of herbage mass: green lamina (inclusive of petiole), green stem (pseudostem, reproductive stem, stolon) and dead tissue in the four treatment swards in period 2 only is depicted in figure 3.3.6.1. The proportions of stem and dead tissue increased as sward herbage mass increased.

Green lamina mass (GLM) was related to total herbage mass (HM) for period 2 only (figure 3.3.6.2) by equation 3.3.6.1, a rectangular hyperbola function.

$$GLM = \frac{1}{0.00151\ (\pm 0.00017) + \frac{0.9391\ (\pm 0.1641)}{HM}} \qquad \ldots\ 3.3.6.1$$

$R^2 = 0.95^*$, n = 4.

A linear function accounted for less of the total variation (0.91 vs 0.95).

Mean green lamina bulk densities for the total sward for period 2 only derived from the canopy structure (figure 3.3.6.1) and the mean sward surface heights (table 3.3.2.1) decreased with

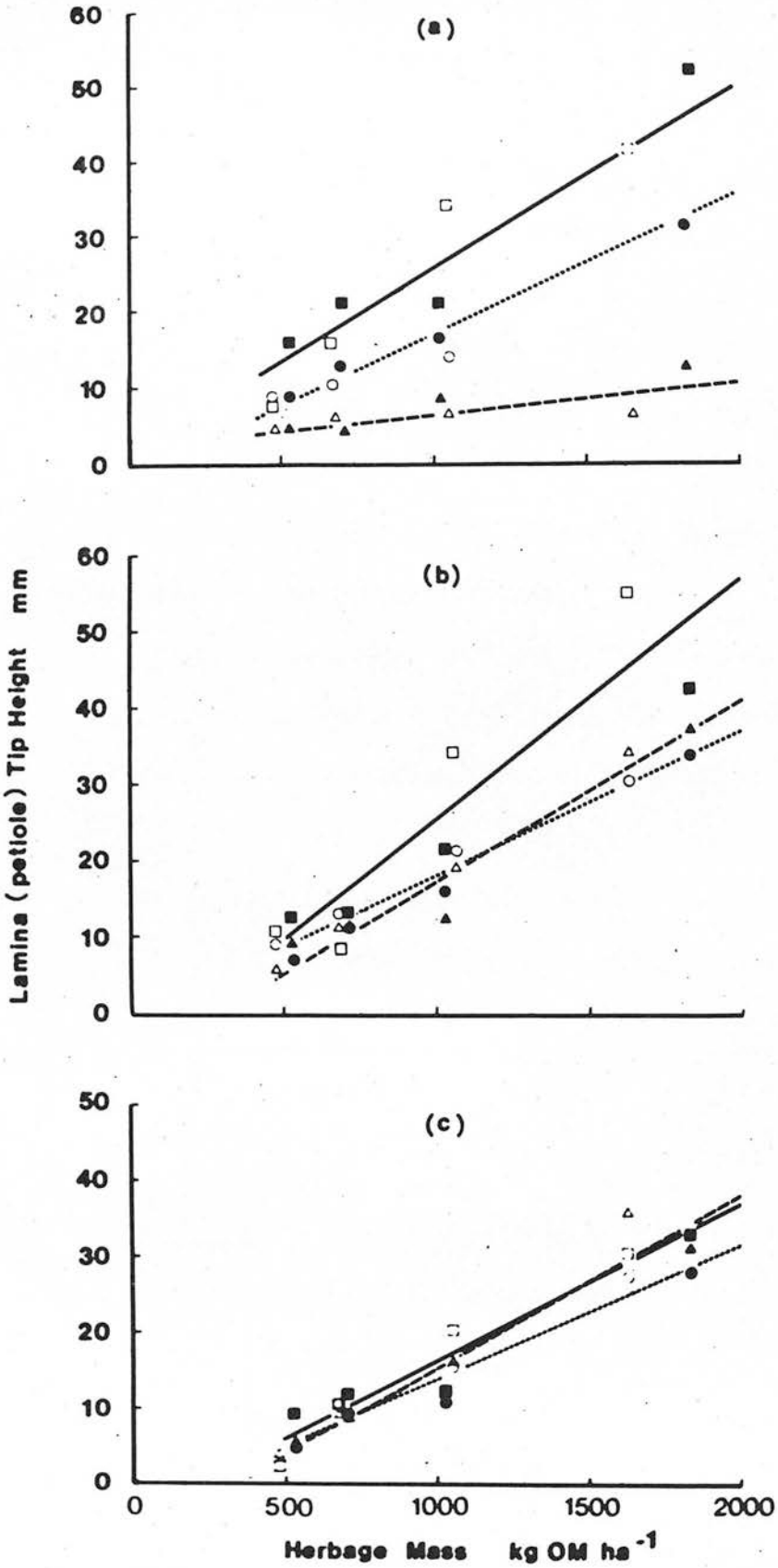

Figure 3.3.6.3 The relationships between lamina (petiole) tip height (mm) above the soil surface for ryegrass (■—□), Poa annua (●·· ○) and white clover (▲---△), and herbage mass. (a) youngest lamina (petiole), (b) penultimate youngest lamina (petiole) and (c) the third lamina (petiole).

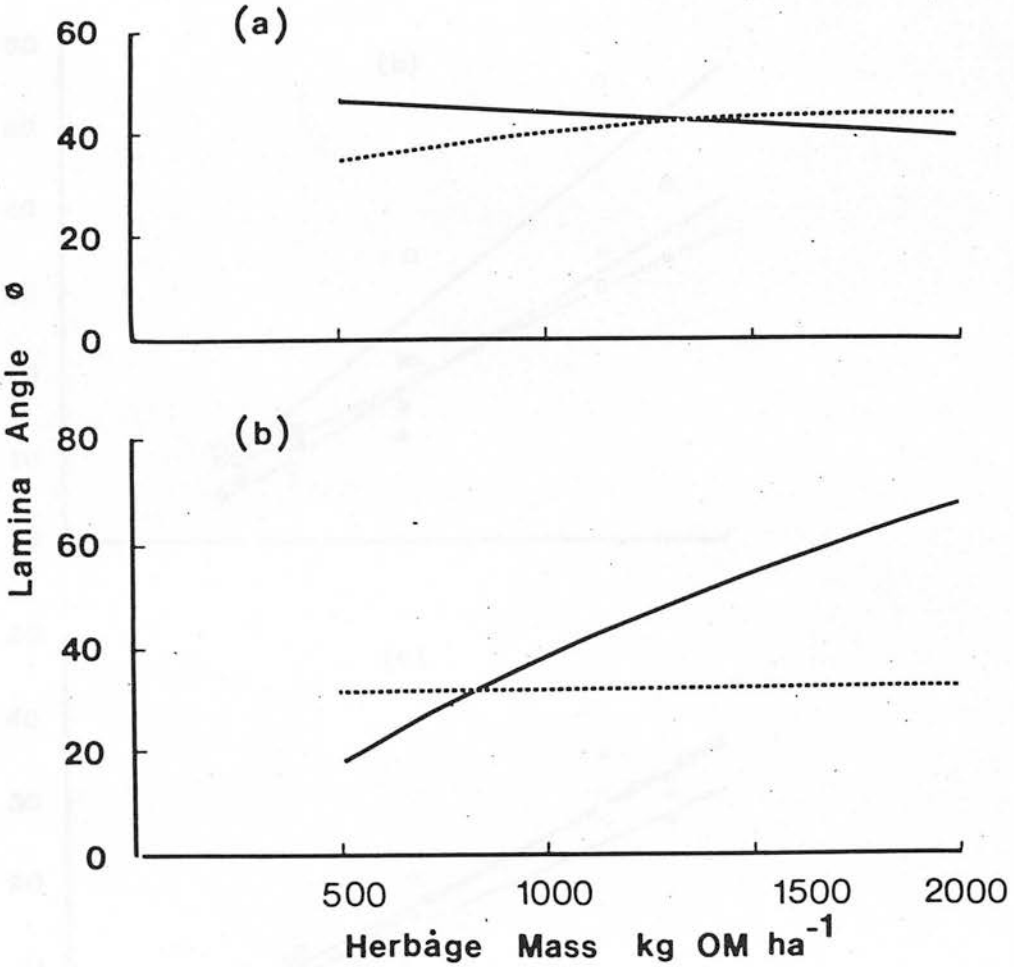

Figure 3.6.6.4 The relationships between foliage angles for ryegrass (——) and Poa annua (·····) and herbage mass. (a) youngest lamina and (b) penultimate youngest lamina.

increasing herbage mass; 641, 484, 404 and 157 kg DM ha^{-1} cm^{-1} for the 500, 700, 1000 and 1700 treatments respectively.

The required botanical dissections for canopy structure determination were performed in period 2 only (section 3.2.5.4).

3.3.6.2. Canopy Geometry

The height of the tips of all laminae (petioles) of equivalent age rank increased with herbage mass (figure 3.3.6.3). The tips of the youngest ryegrass laminae were higher in the canopy than those of Poa and the youngest clover petioles were close to the soil surface. The tips of the penultimate youngest laminae (petioles) were approximately similar in the 500 treatment but in the other treatment swards the tips of the ryegrass laminae were higher in the canopy than the Poa laminae and white clover petioles. The position of the third (one = youngest) laminae (petioles) in the canopy were similar for all three species.

The foliage angles (angles subtended by laminae to horizontal) for the youngest and penultimate youngest laminae, calculated from regressions for lamina tip height, lamina length and penultimate youngest leaf ligule height in relation to herbage mass (equation 3.3.6.2) are depicted in figure 3.6.6.4.

$$\text{Foliage angle} = \text{Sine}\left[\frac{\text{Lamina tip height - ligule height}}{\text{Lamina length}}\right] \quad \ldots 3.3.6.2.$$

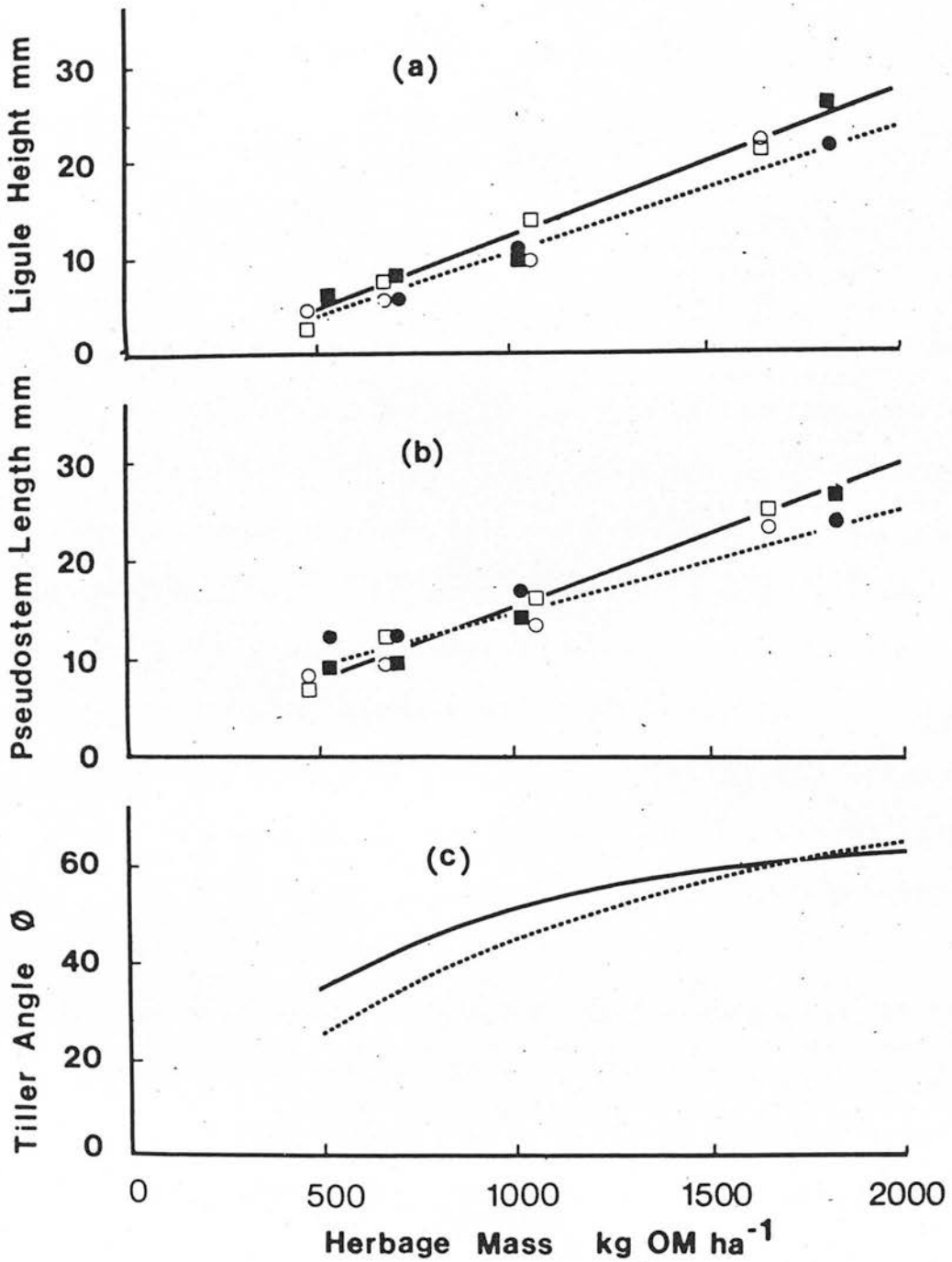

Figure 3.3.6.5 The relationships between (a) height of the penultimate youngest leaf ligule above the soil surface, (b) length of the pseudostem and (c) tiller angle for ryegrass (■–□) and Poa annua (●···○); and herbage mass.

The youngest laminae of both ryegrass and Poa had foliage angles between 35° and 45°, but whereas the foliage angle of the penultimate youngest Poa lamina remained constant at about 35°, that of ryegrass lamina increased markedly with increasing herbage mass.

Pseudostem length and height of the penultimate youngest lamina increased with herbage mass in a similar manner for both ryegrass and Poa (figure 3.3.6.5). Tiller angle, calculated from the regressions of ligule height and pseudostem length, increased with herbage mass (figure 3.3.6.5).

Details of all regression equations used in this section are given in table 5 of appendix 3.

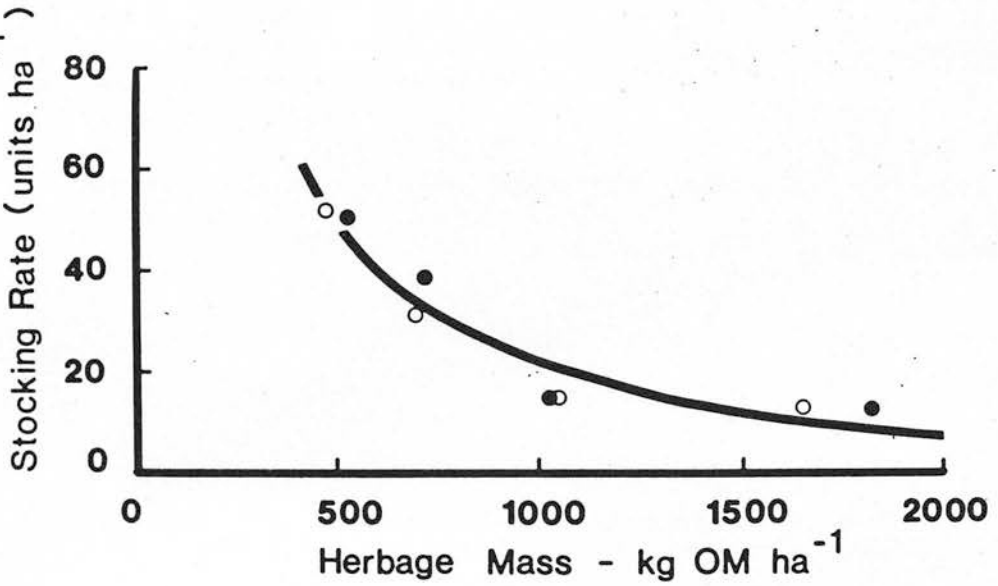

Figure 3.3.7.1 The relationship between stocking rate (SR) (ewes + single lambs) and herbage mass (HM) when the treatment swards were maintained in as near steady state as possible. ($SR = -6.7\ (\pm 4.5) + \frac{28315\ (\pm 3285)}{HM}$, $R^2 = 0.93^{***}$, $n = 8$.

3.3.7. ANIMAL MEASUREMENTS

3.3.7.1 Stocking Rate

The stocking rate of ewes and singles lambs required to maintain the sward conditions of mass and height such that NHA = 0 declined in an asymptotic manner with increasing herbage mass (figure 3.3.7.1).

3.3.7.2 In Vitro Digestibility

In both periods, the organic digestibility of the diet of the ewes was lowest in the 500 and increased in a linear manner to be highest in the 1700 treatment (table 3.3.7.1). The digestibility of the lamb's diet was assumed to be similar to that of the ewes.

Table 3.3.7.1 In vitro digestibility of the diet (ewes)

Treatment	Period 1	Period 2
500	0.719 b[1/]	0.679 b
700	0.785 a	0.751 ab
1000	0.816 a	0.786 ab
1700	0.825 a	0.804 a
Linear component	$P < 0.01$	$P < 0.01$
SE	0.0013	0.0035

1/ Values in columns without common lower case letters are significantly ($P < 0.05$) different.

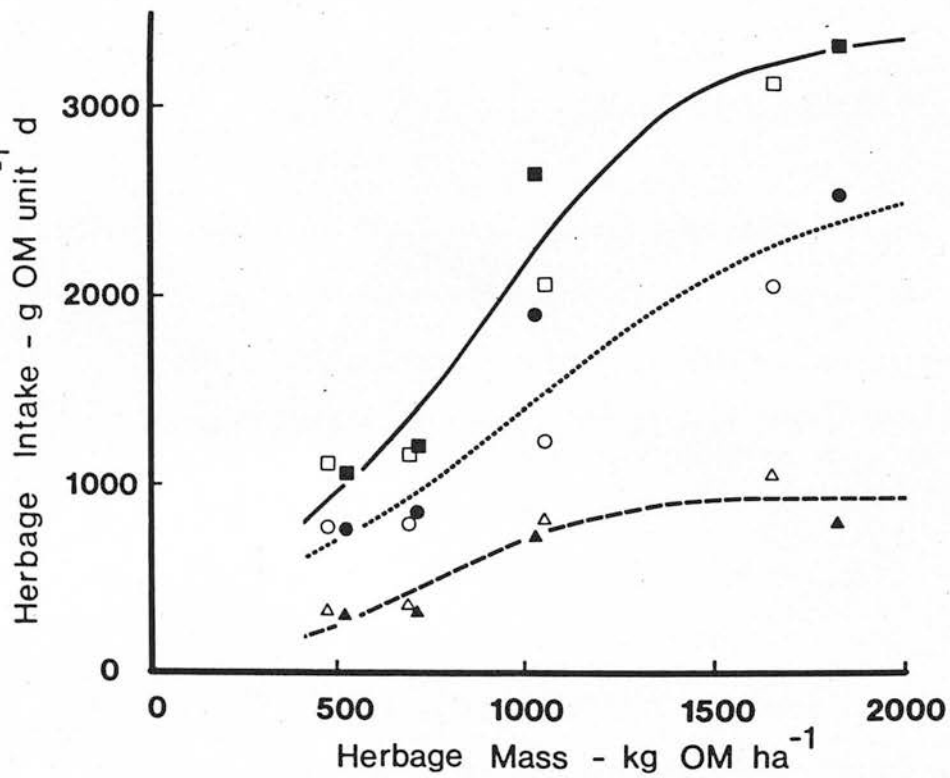

Figure 3.3.7.2 The relationships between organic matter intake for the ewes alone (·····), lambs alone (-----) and ewes and lambs combined (——); and herbage mass.

3.3.7.3 Herbage Intake

Logistic and linear models were fitted to organic matter intake, green organic matter intake and green lamina organic matter intake, for the ewes and lambs separately and ewes plus lambs combined using herbage mass (HM) as the independent variate. All the regression equations are given in tables 6, 7 and 8 of appendix 3.

The logistic model regression equations for total organic matter intake (OMT), ewes alone (equation 3.3.7.1), lambs alone (equation 3.3.7.2) and ewes and lambs combined (equation 3.3.7.3) are depicted in figure 3.3.7.2.

$$OMT_E = \frac{2724\ (\pm 714)}{1 + 9.22\ (\pm 5.55)\ e} - 0.00231\ (\pm 0.0012)\ HM \quad \ldots\ 3.3.7.1$$

$$R^2 = 0.89^{**},\ n = 8.$$

$$OMT_L = \frac{944\ (\pm 90)}{1 + 24.9\ (\pm 23.8)\ e} - 0.00435\ (\pm 0.00138)\ HM \quad \ldots\ 3.3.7.2$$

$$R^2 = 0.88^{**},\ n = 8.$$

$$OMT_{E+L} = \frac{3483\ (\pm 351)}{1 + 11.8\ (\pm 6.3)\ e} - 0.00295\ (\pm 0.00084)\ HM \quad \ldots\ 3.3.7.3$$

$$R^2 = 0.94^{***},\ n = 8.$$

Total organic matter consumption per unit area was highest in the 500 treatment in both periods (table 3.3.7.2).

Table 3.3.7.2 Total organic matter consumption per hectare for ewes plus lambs combined in kg OM ha^{-1} day.

Treatment	Period 1	Period 2
500	54.1 a[1/]	57.6 a
700	46.3 ab	35.7 bc
1000	40.4 b	29.9 c
1700	44.0 ab	40.9 b
SE	3.9	2.5

1/ Values in columns without common lower case letters are significantly ($P<0.05$) different.

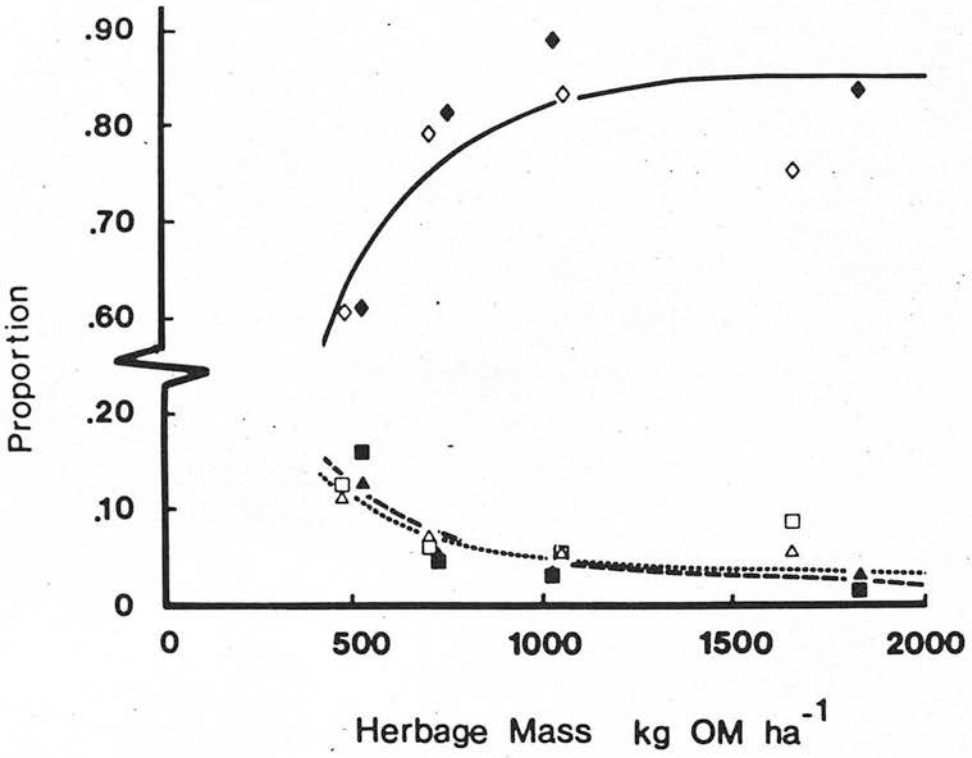

Figure 3.3.7.3 The relationships between the proportions of green grass lamina (◆—◇), green pseudostem (■···□) and dead tissue (▲---△) in the diet of the ewe, and herbage mass.

3.7.7.4 Botanical Composition of the Diet Selected

Rectangular hyperbola models were fitted to the proportions of green grass lamina (GL) (equation 3.3.7.4), stem (pseudostem) tissue (ST) (equation 3.3.7.5) and dead tissue (DT) (equation 3.3.7.6) in the diet of the ewe using herbage mass as the independent variate.

$$GL = 0.88\ (\pm 0.037) - \frac{5.945 \times 10^4\ (\pm 1.5773 \times 10^4)}{HM^2} \quad \ldots\ 3.3.7.4.$$

$R^2 = 0.70^{**}$, n = 8.

$$ST = 0.033\ (\pm 0.0098) + \frac{1.9722 \times 10^4\ (\pm 4.213 \times 10^3)}{HM^2} \quad \ldots\ 3.3.7.5$$

$R^2 = 0.79^{***}$, n = 8.

$$DT = 0.026\ (\pm 0.021) + \frac{2.4538 \times 10^4\ (\pm 9.039 \times 10^3)}{HM^2} \quad \ldots\ 3.3.7.6$$

$R^2 = 0.55^{*}$, n = 8.

A quadratic function also fitted the grass lamina data and accounted for marginally more of the total variation (0.72 vs 0.70).

As herbage mass increased, the proportion of grass lamina in the diet increased to an asymptote whereas the proportions of stem and dead tissue in the diet declined to an asymptote (figure 3.3.7.3). The proportion of clover in the diet exhibited no significant trend.

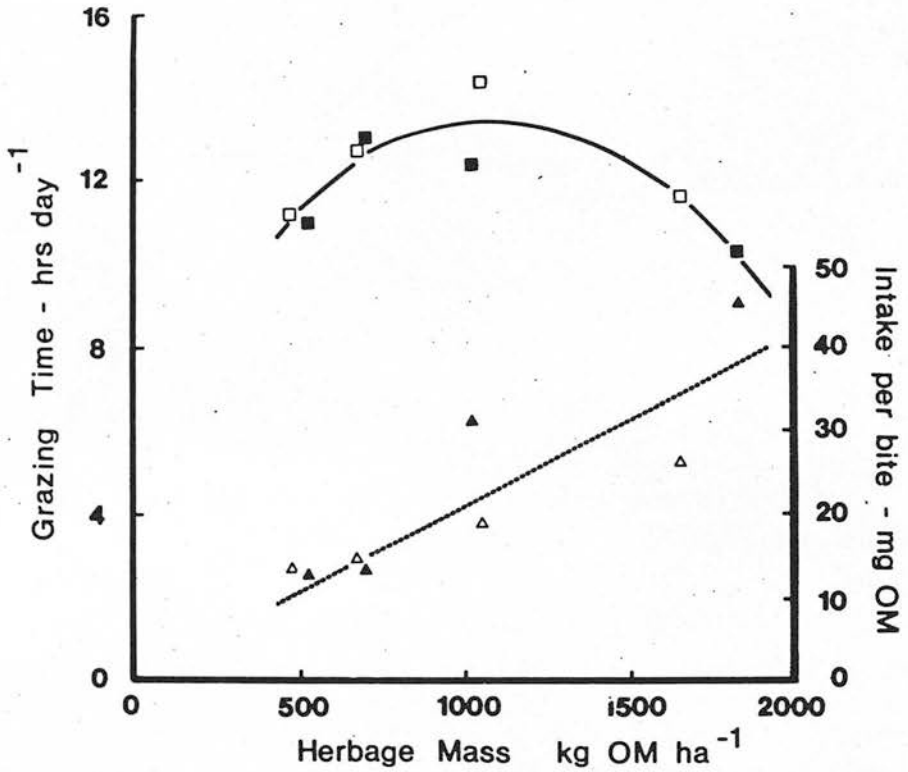

Figure 3.3.7.4 The relationships between grazing time (■—□) and intake per bite (▲...△), and herbage mass.

3.3.7.5 GRAZING BEHAVIOUR

The grazing time (T) of the ewes at first increased, reached a maximum of approximately 13.5 hours per day and then declined as herbage mass increased (figure 3.3.7.4 and equation 3.3.7.7).

$$T = 6.0\ (\pm 1.8) + 0.014\ (\pm 0.004)\ HM - 6.2 \times 10^{-6}\ (\pm 1.5 \times 10^{-6})\ HM^2$$

$$R^2 = 0.78^{*},\ n = 8. \qquad \ldots \quad 3.3.7.7$$

There were no significant differences between the four treatments in the rate of biting in period 1 but in period 2 the rate of biting was significantly higher in the 1700 compared to the other treatments (table 3.3.7.2). The bite rate in the 1700 treatment was significantly higher in period 2 than period 1, there being no significant differences between the two periods for the other treatments. Overall, bite rate was not related to herbage mass.

Table 3.3.7.2 Number of bites per minute for grazing ewes.

Treatment	Period 1	Period 2	Between Periods
500	92.1 a[1/]	88.0 b	n.s.
700	84.0 a	70.5 c	n.s.
1000	82.0 a	76.0 bc	n.s.
1700	89.6 a	112.2 a	* *
SE	6.9	4.2	

1/ Values in columns without common lower case letters are significantly ($P < 0.05$) different.

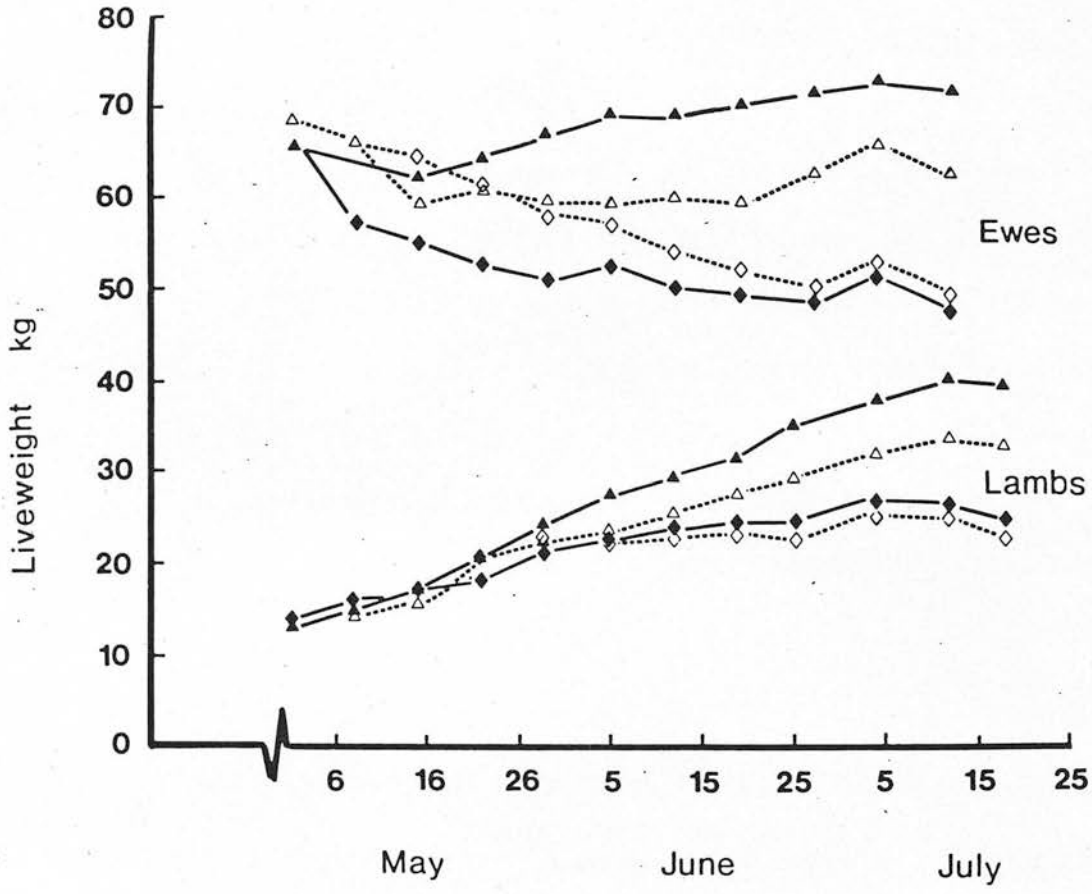

Figure 3.3.7.5 Liveweight change of the ewes and lambs maintained on the 500 (◇···◇), 700 (◆—◆), 1000 (△···△) and 1700 (▲—▲) swards.

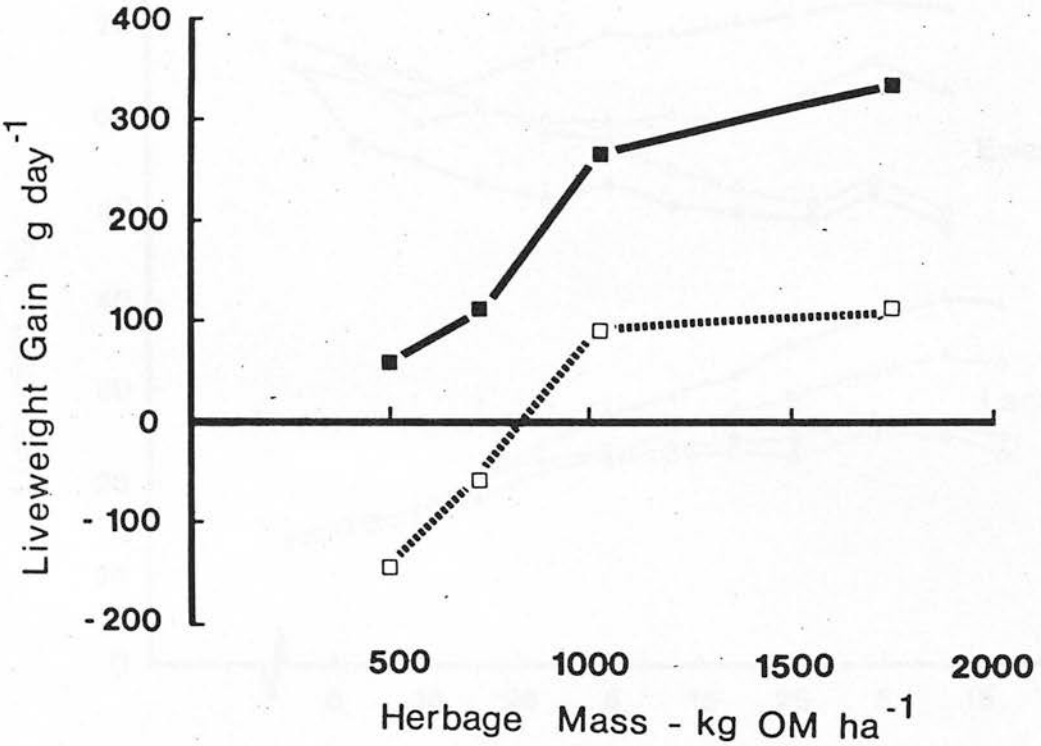

Figure 3.3.7.6 The relationships between liveweight change for the ewes (□···□) and lambs (■—■) and herbage mass between 12th June and 12th July, 1979.

Intake per bite (BS) increased with herbage mass in a linear manner (figure 3.3.7.4 and equation 3.3.7.8).

$$BS = 1.75\ (\pm 5.15) + 0.020\ (\pm 0.005)\ HM \qquad \ldots \quad 3.3.7.8$$

$$R^2 = 0.76^{**},\ n = 8.$$

3.3.7.6 Ewe and Lamb Liveweight

The mean liveweights of the ewes and lambs maintained on treatments for the duration of the experiment are depicted in figure 3.3.7.5.

Ewes on the 500 and 700 treatments lost liveweight between 12th June and 12th July whereas those on the 1000 and 1700 treatments gained liveweight (figure 3.3.7.6). Lamb liveweight gain for the same period increased with herbage mass. Details of liveweight gain are given in table 9 of appendix 3.

3.3.8 RELIABILITY OF THE TILLER MEASUREMENT TECHNIQUE

Three different approaches were used in attempts to establish the reliability of the tiller (stolon) measurement technique adopted in this study.

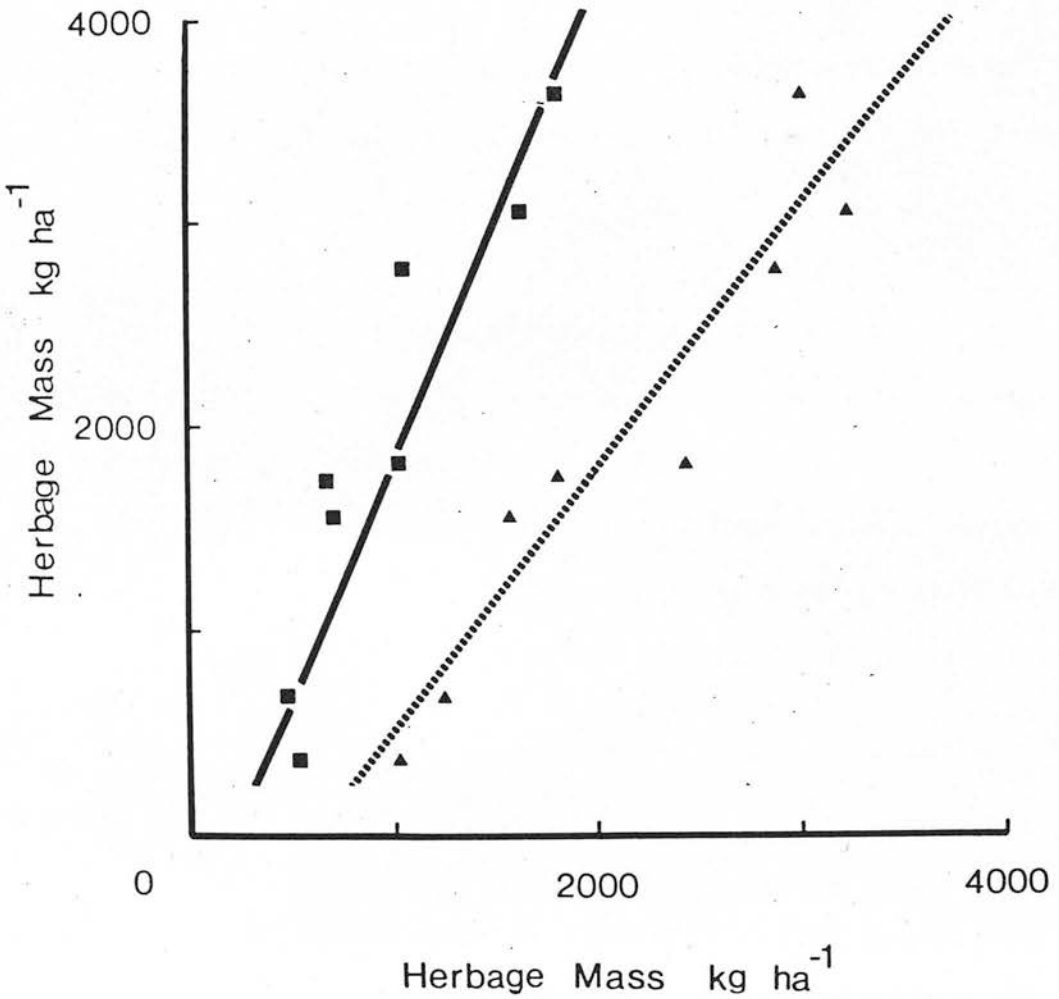

Figure 3.3.8.1 The relationships of herbage mass estimated from tiller (stolon) measurements and herbage mass estimated from field measurements (■—■), and herbage mass estimated from horizon data (▲···▲).

3.3.8.1 Estimation of Herbage Mass

Regression analyses were used to compare the herbage mass of the treatment swards estimated from the individual tiller (stolon) measurements with those estimated from the horizon data (section 3.2.5.4) and field measurements using a shearing hand-piece (section 3.2.5.1).

Herbage mass estimated from the tiller (stolon) measurements (HM_T) and regressed against herbage mass estimated from the field data (HM_F) yielded equation 3.3.8.1 (figure 3.3.8.1).

$$HM_T = -95\ (\pm 37.4) + 2.1\ (\pm 0.34)\ HM_F \qquad \ldots \quad 3.3.8.1$$

$R^2 = 0.86^{***}$, n = 8.

Similarly, herbage mass estimated from the tiller (stolon) data measurements and regressed against herbage mass estimated from the horizon data (HM_H) yielded equation 3.3.8.2.

$$HM_T = -736\ (\pm 389) + 1.3\ (\pm 0.17)\ HM_H \qquad \ldots \quad 3.3.8.2$$

$R^2 = 0.90^{***}$, n = 8.

3.3.8.2 Estimation of Senescence

Estimates of green lamina consumption (C_L) per unit area were derived from the total intake of organic matter per unit area (table 3.3.7.2) and the proportion of green lamina in the diet. These estimates were then used to obtain independent

estimates of lamina senescence (S_L) where G_L is the growth of green lamina ($S_L = G_L - C_L$). No account was taken of the different units used to express animal intake and tissue turnover in the sward i.e. organic matter and dry matter.

Tissue flow on uprooted tillers cannot be included in overall estimates of tissue turnover using the procedures adopted in this experiment, and in the 500 treatment there was a net loss of ryegrass tillers between the two periods (table 1 of appendix 3) caused by the uprooting of tillers during grazing. The average rate of loss of ryegrass tillers between the two periods was 100 tillers m^{-2} day^{-1} and complete utilisation of the lamina fraction on these tillers was assumed. This assumption enabled the amount of green lamina consumption from uprooted tillers to be estimated at 18.3 and 17.7 kg DM ha^{-1} day^{-1} for periods 1 and 2 respectively. These amounts were deducted from the estimate of green lamina production (animal derived) in the 500 treatment so that the animal and plant measures of tissue turnover were comparable.

Measured lamina senescence rates (S_M) were regressed against lamina senescence rates (S_L) estimated from measured lamina growth rates (G_L) (table 3.3.5.7) and lamina consumption rates (C_L). This analysis yielded equation 3.3.8.3 which was not significant.

$$S_M = 12.1\ (\pm 8.8) + 0.60\ (\pm 0.32)\ S_L \quad \ldots \quad 3.3.8.3$$

$$R^2 = 0.38^{n.s.},\ n = 8.$$

However, when sward measured lamina senescence (S_M) was estimated from equation 3.3.5.5 and regressed against lamina senescence rates (S_L) estimated from lamina growth rates (G_L), themselves estimated from regression equations (table 3.3.5.14), and lamina consumption rates (C_L) the resulting equation (equation 3.3.8.4) was significant ($P < 0.05$).

$$S_M = 3.8\ (\pm 7.8) + 0.89\ (\pm 0.30)\ S_L \quad \ldots \quad 3.3.8.4$$

$$R^2 = 0.59^{*},\ n = 8.$$

The regression coefficient for equation 3.3.8.4 was not significantly different to unity.

Further details are given in table 10 of appendix 3.

3.3.8.3 Estimation of Consumption

Green herbage consumption per unit area was calculated from the total organic matter intake per unit area (table 3.3.7.2) and the proportion of green tissue in the diet. Consumption per unit area can also be calculated by estimating the amount of herbage removed from a sward per unit area per day from the individual tiller and stolon measurements. The procedures for estimating

Table 3.3.8.1 Comparison of animal and sward estimates of consumption (kg OM (DM) ha^{-1} day^{-1}).

Period	Treatment	Consumption Animal	Sward[3/]
1	500	39.7	16.7 + 35.0 [1/]
	700	42.8	47.3
	1000	39.7	58.0
	1700	43.1	43.1
2	500	45.0	17.8 + 41.4[1/]
	700	32.8	34.7
	1000	28.3	43.9
	1700	37.0	25.5
	Mean	38.6	45.4 t = 1.51[n.s.]
	SE	3.4	6.8 df = 7[2/]

1/ 35.0 and 41.4 kg DM ha^{-1} day^{-1} added to sward estimates of consumption. See text in section 3.3.8.3.

2/ Because the variances were unequal 7 degrees of freedom only were used (Snedecor and Cochran, 1967).

3/ The means and standard errors of the means of the parameters used to calculate these data can be found in tables 11 and 12 of appendix 3.

the required parameters were detailed in section 3.2.8. As in the previous section, allowance was made for the net loss of ryegrass tillers in the 500 treatment, but instead of green lamina the entire green fraction of these tillers was assumed to be consumed by the grazing animal. On this basis, 35.0 and 41.4 kg DM ha^{-1} day^{-1} were added to the sward estimates of consumption for the 500 treatment in periods 1 and 2 respectively. As in the previous section no account was taken of the different units used for the animal and sward estimates of consumption. Further detail is given in tables 11 and 12 of appendix 3.

Correlation - regression analysis proved impractical as a means of comparing the estimates of consumption because of the small range in consumption and the variability of the sward estimates of consumption. Instead, the null hypothesis that animal and sward estimates should be similar was examined. There was no significant difference between the estimates of consumption (table 3.3.8.1).

3.4. DISCUSSION

3.4.1 STATISTICAL PROCEDURES

The major statistical problem was the absence of treatment replication. The problem that arises through lack of replication is the possibility that one treatment may have a higher or lower potential growth rate than another due to, for example, higher natural soil fertility or better soil moisture retention characteristics. The most important sward in the experiment was the 1000 treatment in that, irrespective of the model of growth adopted, this sward was at or near the point of inflexion. If growth rates in this treatment were naturally higher or lower than those in the other treatments under similar conditions, then the growth models depicted in figures 3.3.5.1 - 3.3.5.3 may be distorted.

The 1000 and 500 treatments were originally parts of the same paddock and the 1700 and 700 treatments part of another paddock. Total growth rates per primary ryegrass tiller in the 500 and 700 treatments were not significantly different. Total growth rates per primary ryegrass tiller in the 1000 and 1700 treatments were also not significantly different. Therefore, the potential growth rates in all four treatments under identical management are likely to have been the same. Estimates of per unit area lamina growth, total growth rates etc. differed between quarters of paddocks (significant quarter main effects) and the absence of significant treatment x quarter interaction in the per unit area data suggests that the pattern of variation was similar in all treatments. The four treatment paddocks

were therefore similar and the contention that treatment effects swamped any residual differences between treatments has considerable support from the data. It is considered, therefore, that the results can be treated with confidence.

The period x treatment x species interaction for net production per primary unit and per unit area was not significant ($P > 0.05$) but the first order interaction terms for all other parameters in both per primary unit and per unit data were significant ($P < 0.01$). The main effect terms for period, treatment and species were therefore of limited interpretive value and accordingly period x treatment x species interaction tables have been used throughout to present both the per primary unit and per unit area data.

In the per unit area interaction tables (tables 3.3.5.9 - 3.3.5.13), the clover means were small compared to those of the grasses and the LSD values bigger than these means. At first sight this would seem to be a serious limitation but inspection of the clover means revealed that their ranges were small. The overall contribution of clover was only 0.06 of total net production and it was considered that between treatment comparisons for clover were unimportant in this context.

3.4.2 THE TILLER (STOLON) MEASUREMENT PROCEDURE

The procedure of tiller measurement pioneered by Hodgson (1966) and adopted by Hodgson and Ollerenshaw (1969), McIvor and Watkin (1973), De Lucia Silva (1974) and Wade (1979) was developed to the

point where growth, senescence and net production for individual pasture species could be expressed in mass units either per individual tiller or stolon (μg DM tiller (stolon)$^{-1}$ day^{-1}) or per unit area (kg DM ha^{-1} day^{-1}). It was considered that if reliable estimates of tissue turnover could be obtained, then an alternative field procedure to that described by Wiegert and Evans (1964) existed which would allow the many aspects of the sward-animal interface to be examined. Both the Wiegert and Evans (1964) technique and its modification (Lomnicki, Bandola and Jankowska, 1968) depend upon accurate estimates of the rate of disappearance of dead tissue. The requirement of these techniques for paired plots, the removal of all the living or all the dead tissue in situ and the necessity to make a number of assumptions (Lomnicki et al, 1968), can make accurate estimates of the rate of dead tissue disappearance difficult to obtain. The tiller measurement technique described in this study also involves a number of assumptions but it has two important advantages which are particularly relevant to the understanding of the sward-animal interface : (1) it utilises senescence rather than disappearance rates in calculating tissue turnover ; and (2) response per unit area is partitioned between individual plant unit and population density. Not only is senescence rate easier to calculate than disappearance rate but information on senescence rate enables comment on the utilisation of individual species in a mixed species sward. The Wiegert and Evans (1964) based techniques cannot do this because the source of dead material cannot always be ascertained. The dynamics of the reaction of a grazed sward to the grazing animal cannot be properly understood without information on individual plant unit and population density response and the Wiegert and Evans (1964) based techniques cannot provide this information either.

The tiller measurement technique also has the advantage that repeated measurement of the same sample unit can reduce error (Davies, 1981).

The estimation procedure for the tiller measurement technique from the initial field measurements of linear dimensions to the final estimates of growth, senescence and net production rates involves the use of multiplicative constants and regression equations to correct empirically calculated values to estimates of absolute values.

Grass lamina area was calculated by multiplying field measurements of lamina length by mean breadth values and then correcting the area estimate by linear regression equations (section 3.2.5.5). These equations accounted for 0.89 - 0.96 of the total variation and were therefore used with some confidence. An attempt was made to allow for folding of the youngest lamina by using a separate mean breadth value for this leaf which was also used for daughter lamina tissue.

The estimation of clover lamina area was more prone to error because first a potential area was calculated from petiole length using a power law regression equation (section 3.2.8), which was reduced by the amount of lamina estimated to be missing. This equation accounted for 0.69 of the total variation and included lamina in all stages of growth. Carlson (1966) reported that lamina area increased with petiole length but did not derive a mathematical relationship. This is a source of error that cannot be easily overcome unless a better relationship can be obtained.

The next source of possible error in the procedure arises when lamina mass is estimated from lamina area by multiplying by a lamina weight per unit area constant. Senescence rate, for example, could be overestimated by using a constant derived from the youngest fully expanded leaf, a danger recognised by Robson and Deacon (1978) and avoided by Williamson (1976) who assumed that all leaves except those dying were expanding. In this study a separate weight per unit area constant was calculated for the youngest lamina on primary grass tillers and this constant also used for daughter tiller lamina tissue. A single weight per unit area constant was used for all remaining lamina tissue. The folded nature of the youngest expanding lamina was the reason for calculating a separate constant for this tissue. The sample for the youngest lamina constant included rapidly expanding and mature, but still the youngest, lamina. Similarly the constant for all the remaining laminae was derived from fully expanded leaves and the green fraction of leaves that were senescing. Both weight per unit area constants were therefore average values for leaves in a range of conditions. The overall mean weight per unit area constant for all ryegrass laminae except the youngest was 33.9 ± 1.26 μg DM mm^{-2} which compares well with a value derived from De Lucia Silva's (1974) data. De Lucia Silva (1974) quoted a weight per unit length constant for mature ryegrass lamina of 68 μg DM mm^{-1} which if a mean lamina breadth of 2.0 mm (overall average for ryegrass in this experiment was 1.9 ± 0.07 mm) is assumed gives a weight per unit area value of 34 μg DM mm^{-2}.

There must be errors associated with the estimation of both growth and senescence in the tiller measurement procedure because no

account is taken of the weight changes that occur throughout the life of a leaf. Thus Vine (1977) found that on average 0.4 of the weight of a fully expanded leaf was lost between full expansion and time two leaf appearance intervals later, weight loss varying between 0.2 and 0.6 depending on season. Robson and Deacon (1978) reported a weight loss of 0.3 of the fully expanded leaf weight between full expansion and leaf death. However, the use of average,and not maximum or minimum, values for these constants probably enabled reasonably accurate estimates of average growth and senescence rates on an individual plant unit basis to be made.

For clover a single weight per unit area constant was used for all laminae. A separate constant for the youngest lamina was used initially but was found to be impractical because of the analytical procedures used (section 3.2.8). When the youngest petiole and lamina unit was superceded by another, weight loss could occur in the penultimate youngest unit because of the change over in the constants. This artifical condition was considered unsatisfactory and a single overall constant was used which probably resulted in slight underestimation of growth rates. For both grasses and clover, the use of mean values resulted in overestimation of growth rate during early expansion and underestimation of growth rate later etc..

The final step of the procedure involved multiplying the individual plant unit growth or senescence values by a constant derived from the population density data to obtain per unit area values. Clearly, this step could result in substantial error if the estimates of population density were for any reason greatly different from the

actual population density. For example, the high total growth and senescence per unit area estimates for Poa in the 700 treatment in period 1 (tables 3.3.5.7 and 3.3.5.12) could be due to a high estimate of Poa population density for this treatment (table 1 of appendix 3). Patchiness in the sward due to uneven harvesting by the grazing animal is a source of potential error in population density estimates especially when sample numbers are small.

The tiller measurement procedure as used in this experiment relied upon a single estimate of population density. However, if the population dynamics of the sward are such that there is a net loss of tillers or stolons due to an external factor such as uprooting, then the procedure as it stands cannot accurately estimate tissue fluxes. A net loss of ryegrass tillers, approximately 100 tillers m^{-2} day^{-1} between the two periods, occurred in the 500 treatment. In this circumstance where population density was estimated approximately mid-way through the experimental period, per unit area estimates of growth may have reflected average growth rates for the period but senescence rates were almost certainly underestimated. Underestimation of senescence must have occurred because not all the uprooted tillers were consumed by the grazing animals and senescence rate on these tillers was not measured. Net production rates must therefore have been overestimated in the 500 sward. Tiller fluxes would have to be measured to surmount this problem.

All three evaluations of the tiller measurement technique (section 3.3.8) suggest that it provided useful estimates of tissue turnover. Thus in static terms, herbage mass calculated from the horizon data reliably estimated herbage mass estimated from the tiller

data (R^2 = 0.90***) and the regression coefficient (1.3 $\pm$ 0.17) was greater than unity but not significantly so. A value less than unity for this coefficient could be expected because the horizon estimates of herbage mass included dead tissue whereas the tiller estimates were of green herbage only. The extreme shortness of the 500 treatment sward made it difficult to obtain horizon herbage samples which did not include root tissue and soil. Also, the horizon sampling procedure did not include determination of organic matter content and although an attempt was made to dissect out all the root tissue and to remove the soil by washing, it is likely that quantities of both remained. Therefore the horizon sample estimates of herbage mass on the 500 treatment may have been overestimated. When the 500 treatment was excluded from the analysis the value of the regression coefficient was reduced (1.10 $\pm$ 0.29**).

The high regression coefficient (2.1 $\pm$ 0.34) for the relationship between tiller estimates (dependent variable) and field estimated (independent variable) herbage mass was not surprising in view of the fact that considerable stubble remains even after cutting to nominal ground level with a shearing hand-piece. It was also difficult to ensure that none of the harvested material was lost during the picking up process.

A more rigorous test of the reliability of the tiller measurement technique was to assume that NP = G - S = C (equation 3.1.2). This was done for lamina only and senescence estimated indirectly by inserting animal derived estimates of green lamina consumption into equation 3.1.2. When measured values of lamina growth and senescence were used, the regression of directly measured senescence on indirectly

measured senescence was not significant. However, when lamina growth and senescence rates were themselves estimated from regression equations, the regression of directly on indirectly estimated senescence was significant ($R^2 = 0.59^*$) and the regression coefficient (0.89 ± 0.30) was not significantly different from unity. Significant departure from unity would indicate that the tiller measurement technique as implemented in this study did not accurately describe tissue turnover.

The most rigorous of the three tests of the reliability of the tiller measurement technique was to compare consumption as estimated through the animal against that estimated through the sward. This test was also the one most prone to error because the sward estimates of consumption were dependent upon accurate measures of the tissue removed per plant unit per defoliation and interval between successive defoliations. The latter becomes increasingly difficult to estimate accurately as the interval between successive defoliations approaches the length of the measurement period. Higher values for sward estimates could be expected because of grazing by invertebrates or other grazing animals such as rabbits and hares. There was no evidence that non-agricultural animals were important and though sward estimates of consumption were higher than the animal estimates (45.4 ± 6.8 vs 38.6 ± 3.4 kg DM (OM) ha^{-1} day^{-1}), the difference was not significant.

Patterns of tissue flow derived from tiller measurement and carbon exchange techniques are comparable (Hodgson et al, 1981) which together with the above evaluations suggests that the tiller measurement technique gives reasonably consistent estimates of tissue

turnover. In swards of herbage mass less than 650 kg OM ha^{-1} such as the 500 treatment in this study, which may be unstable, the technique may be less reliable underestimating senescence and overestimating net production.

3.4.3 SPECIES PRIMARY TILLER (STOLON) PERFORMANCE

Overall, primary ryegrass tillers had higher lamina growth, pseudostem growth and total growth rates (table 3.3.5.3) than primary Poa tillers ; senescence rates were similar. In monocultures, the yields of ryegrass and Poa can be similar but in mixtures of the two species, the yield of Poa is reduced (Wells, 1974 b). In this experiment, the two youngest ryegrass laminae were higher in the canopy (section 3.3.6.2) than comparable Poa laminae, the ryegrass laminae almost certainly shading the Poa laminae. The photosynthetic capacities of Poa laminae, if they reacted to shading in a similar manner to ryegrass, would therefore have been reduced (Woledge, 1978). Above a herbage mass of approximately 1200 kg OM ha^{-1}, the penultimate youngest clover laminae were also higher in the canopy than Poa laminae. The youngest clover laminae were clearly shaded by the remainder of the canopy but overall lamina, stolon and total growth rates for clover were higher than those for both ryegrass and Poa. Clover laminae can have photosynthetic capacities similar to those of ryegrass (Dennis and Woledge, 1979) but whereas the photosynthetic capacity of ryegrass lamina shaded during expansion falls (Woledge, 1978) clover laminae do not appear to suffer as much of a drop in

photosynthetic capacity, probably because they remain folded until their petiole has pushed them into a region of adequate light. The generally higher rates of tissue growth on the terminal growing point of clover compared to individual ryegrass tillers may reflect this greater photosynthetic capacity in the higher mass swards. Overall, total growth rate per unit lamina area was highest for white clover followed by ryegrass and then Poa (6.74, 3.41 and 2.17 μg DM mm^{-2} day^{-1}). Another significant factor may be the greater ($P<0.05$) number of growing petiole plus lamina units than growing laminae on marked stolon units than ryegrass tillers (1.70 vs 1.26 $\pm$ 0.04).

For all three species lamina growth, pseudostem (stolon) growth and total growth rates per primary tiller (stolon) tended to increase with herbage mass (tables 3.3.5.4 - 3.3.5.6) as did leaf area per primary tiller (stolon) (table 3.3.5.1). Both ryegrass and white clover total growth rates per primary tiller (stolon) were linearly correlated with leaf area per primary tiller (stolon) ($R^2 = 0.62^*$, $R^2 = 0.82^{**}$ respectively) but Poa total growth rates were not. With the exception of the 1700 treatment in period 1, all three species in each treatment had similar leaf areas per primary tiller but different photosynthetic capacities (see previous paragraph). Therefore, the use of leaf area alone in a mixed species sward as an index of species growth potential is clearly limited.

In period 1, the total growth rates of Poa primary tillers in the 500 and 1700 treatments were significantly lower than those in the 700 and 1000 treatments and also the rates measured in period 2 in the 500 and 1700 treatments. In the 1700 treatment, the reproductive stem development that occurred between the two periods may have meant

that primary Poa tillers were able to exploit a more favourable light environment. Provided that the inflorescence was exposed to light, the position of the laminae in the canopy may not matter as much as for vegetative tillers because inflorescence tissue can account for more than 0.5 of total assimilation in both ryegrass and Poa (Ong et al, 1978). This argument cannot be used to account for the higher Poa primary tiller total growth rate in the 500 treatment in period 2 than period 1 because the vegetative Poa tillers in the 500 treatment suffered little from shading by ryegrass (figure 3.3.6.3). It is possible that the very low total growth rates of primary Poa tillers in the 500 treatment in period 1 represent the reaction of vegetative Poa tillers to frequent defoliation. Leaf areas per primary Poa tiller in both periods were virtually identical and it may be that once reproductive growth had commenced, removal of lamina did not have as great an effect on total growth rate because the inflorescence also produced assimilate.

Primary tiller total growth rates were lower in Poa than in ryegrass (table 3.3.5.6), and this difference occurred mainly in the 1000 and 1700 treatments. With the exception of the 500 treatment in period 1, Poa primary tiller total growth rates were similar in the 500 and 700 treatments which suggests that within-canopy shading by ryegrass and white clover was not as severe in these two treatments.

Clover senescence rates were significantly lower than those of both ryegrass and Poa overall (table 3.3.5.3). This phenomenon can probably be attributed to the morphology of white clover whereby the

petioles subtended their laminae into the grazed horizon. When defoliation took place it is likely that all the lamina present was removed and only petiole tissue, which was on average 0.23 of the combined petiole plus lamina weight, remained to senesce. Whenever lamina tissue remains undefoliated, as it did in the 1700 treatment in period 1, higher senescence rates are likely (table 3.3.5.7).

Ryegrass and Poa primary tiller senescence rates were similar (90 vs 84 $\pm$ 6.3 μg DM tiller^{-1} day^{-1}) but total growth rates were higher in ryegrass (258 vs 162 $\pm$ 12.9 μg DM tiller^{-1} day^{-1}). Therefore the S : G ratio for ryegrass primary tillers was lower than that for Poa primary tillers (0.35 vs 0.52). In this experiment, where NHA = 0 and C = G - S (equation 3.1.2), C/G = 1 - S/G and the C : G ratio is a measure of utilisation efficiency. Clearly the utilisation of the tissue grown was much higher for ryegrass than Poa (0.65 vs 0.48) and this reflected the higher position of the youngest and penultimate youngest ryegrass laminae in the canopy, and also the greater foliage angle of the penultimate youngest ryegrass laminae. The lower frequency and severity of defoliation that primary Poa tillers were subjected to compared to ryegrass supports this contention (tables 11 and 12 of appendix 3).

3.4.4 PLANT COMPETITION

The effects of competition for light on the growth rates of the three species were discussed in the previous section but competition also determines which species will persist in a sward (section 2.3).

Grime's (1974, 1977) triangular ordination model suggests that a competitive species like ryegrass should have a proportionately higher population density in the least disturbed swards. Without doubt the 1700 treatment sward was the least disturbed and the mean proportions of ryegrass and Poa respectively, on a population density basis, were 0.65 and 0.28 compared to 0.56 and 0.42 in the 700 treatment. Increasing the degree of disturbance reduced the competitiveness of ryegrass not only because its total growth rate per tiller was reduced but because its ability to shade and restrict the growth of Poa tillers was also reduced. According to Grime (1977), species such as Poa annua, exhibiting the ruderal strategy in response to severe disturbance, are successful because they are free seeders. Poa annua, for example, can have much higher buried seed reserves than ryegrass (Thompson and Grime, 1979) which allows it to exploit areas of bare ground caused by urine burn or treading damage etc.. Poa ingress into established pasture often follows a period of intensive grazing (Wells, 1974 a) and if the population density of the resident species is reduced by uprooting, for example, the buried seed reserves of Poa give it a significant advantage.

It is possible to conclude that Poa annua is found in heavily grazed swards because it is more tolerant of such conditions than ryegrass. The evidence from this experiment suggests that Poa annua, rather than being a grazing-tolerant species, is in reality a grazing-evasive species because, in continuously stocked mixed species swards at least, it retains leaf area and mass by maintaining a foliage angle lower than its competitors and by making its leaf mass less accessible to defoliation.

Within-species competition for space (White and Harper, 1970 ; Kays and Harper, 1974) also occurred, with population density falling as herbage mass increased (figure 3.3.3.1). Over a range of continuously stocked swards including the 700, 1000 and 1700 treatment swards of this experiment, Hodgson et al (1981) found that the exponent 'b' in the relationship, $y = ax^b$ where 'y' is the weight of an individual tiller and 'x' is the population density, varied between - 1.2 and - 1.7 in four separate studies and did not differ significantly from the value of - 1.5 proposed by Yoda et al (1963). Clearly this relationship broke down below a herbage mass of 700 kg OM ha^{-1} principally because the rate of loss of tillers was greater than the rate of appearance of new tillers i.e. the sward was unstable.

The population density of white clover was very low in all treatments and overall its per unit area contribution to net production was 0.06 of the total. However, it has been suggested that even small amounts of clover in the sward are valuable in animal production terms because of its superior feeding value (Thomson, 1978). White clover has been described as a very mobile plant wandering within a sward composed of more static grass clones (Harper, 1978). Harper (1978) envisaged white clover as having an escapist form of growth in which individual genets were continuously tracking a favourable mosaic of ecologically compatible companion grasses. However, as Harper (1978) puts it, tracking may also be necessary for the continued survival of a particular genet in that the greater the distance between stolon internodes and therefore potential petioles, the more remote is the possibility that all the laminae on one stolon are defoliated at the same time, thus ensuring continued assimilate supply. In the 500

and 700 treatments the morphology exhibited by white clover was that of small laminae and much axillary branching (Kydd, 1957 ; Davidson and Birch, 1972 ; Pascoe, 1973 ; Suckling, 1976) with only small distances between stolon internodes. Stolon growth rate as measured in this experiment combined mass change due to extension and mass change due to assimilate storage, and in the 500 and 700 treatments was much reduced compared to that in the 1700 treatment. The opportunity for complete defoliation of a white clover genet must be enhanced when its tracking ability is reduced and its chances of survival diminished.

3.4.5 PER UNIT AREA PERFORMANCE

It must be emphasised again that because of the methods adopted in this study primary tiller (stolon) performance cannot be multiplied by species population density (sum of primary + daughter units) to obtain per unit area performance. The method adopted (section 3.2.8) was to multiply the primary plus daughter parameter values per primary unit locus by the species density of the primary units only.

3.4.5.1 Individual species

In general terms, species performance per unit area is the product of individual tiller or stolon performance and the population density of the species, and the combined species (sward) performance per unit area is the sum of the individual species performances per unit area.

Thus the response of a sward to a particular management may involve: (1) changes in the species population densities ; (2) changes in the performance of the individual tiller of stolon : or (3) changes in both (1) and (2). In period 2, for example, the higher per unit area total growth rate for ryegrass in the 700 compared to the 500 treatment was due primarily to the higher population density of the ryegrass in the 700 treatment. The non-significant increase in Poa per unit area total growth rate in period 2 between the 700 and 1000 treatments was due primarily to an increase in individual tiller total growth rate. Also, the big difference in ryegrass per unit area total growth rate between the 700 and 1000 treatments in period 2 (46.2 vs 81.5 $\pm$ 12.7 kg DM ha^{-1} day^{-1}) was achieved by a higher tiller growth rate (131 vs 401 $\pm$ 104.1 ug DM $tiller^{-1}$ day^{-1}) despite a lower population density (37400 vs 23833 $\pm$ 2642 units m^{-2}). This illustrates the flexibility of adaptation in a mixed species sward.

3.4.5.2 Combined species

Irrespective of the model adopted, the combined species total growth rate of the sward increased rapidly over a small range of herbage mass to approach or reach a maximum value (figures 3.3.5.1 - 3.3.5.3) at a herbage mass of approximately 1000 kg OM ha^{-1}. The maximum predicted total growth rates of between 106.1 $\pm$ 3.1 and 117.7 $\pm$ 5.4 kg DM ha^{-1} day^{-1}, depending on the model adopted, compare well with those of Tainton (1974) for a mixed species sward in late spring - early summer which was rotationally grazed with sheep (123 - 128 kg DM ha^{-1} day^{-1}) and that of Morris (1970) for

cut cocksfoot swards in mid-summer (100 kg DM ha^{-1} day^{-1}). Galbraith, Arnold and Carbon (1980) constructed a pasture growth model for their mediterranean climate in which the maximum growth rate of 126 kg DM ha^{-1} day^{-1} was achieved at a herbage mass of approximately 2300 kg DM ha^{-1}.

Estimates of senescence rates in this experiment ranged between 11 and 42 kg DM ha^{-1} day^{-1} and these too compare well with the few values reported in the literature. Thus, Tainton (1974) reported senescence rates in mixed species swards of 23 - 31 kg DM ha^{-1} day^{-1} and Wade (1979) calculated values of 42 - 48 kg DM ha^{-1} day^{-1} for ryegrass swards rotationally grazed with sheep from De Lucia Silva's (1974) data and also values of 9 - 24 kg DM ha^{-1} from his own experiment on ryegrass swards rotationally grazed with dairy cows.

Net production rates derived from logistic models of net herbage accumulation over time increase to a maximum and then decline (Davidson and Donald, 1958 ; Noy-Meir, 1975). For the net production function to have this form, senescence must progressively increase relative to growth rate such that the two functions intersect at some point where $NP = G - S = 0$. A variety of growth and senescence functions could be used to conform to the above requirements but under the continuous stocking management of this experiment a growth model with an asymptote and a linear model for senescence satisfied this requirement.

Of the three growth models described, the logistic model fitted the data best and is perhaps conceptually the best in that it effectively passes through the origin which the rectangular hyperbola

and piece-wise linear models do not. However, without data points between zero and 500 kg OM ha^{-1} herbage mass, the correct shape of the growth model cannot be determined and to reduce herbage mass below 500 kg OM ha^{-1} in a temperate environment may be extremely difficult without incurring severe penalties in animal performance. In annual swards in mediterranean environments, levels of herbage mass below 500 kg OM ha^{-1} can be achieved (Greenwood and Arnold, 1968) through low population densities.

The two linear models used to describe the relationship between rate of senescence and herbage mass, one inclusive of an aberrant data point and the other excluding this point, were not significantly different and seemed appropriate in view of Wade's (1979) findings that senescence increased in a linear manner during regrowth. Also, a superficial reappraisal of Hunt's (1971) data suggested that a linear model would probably have fitted up to day 60. The data point which upsets the fit of the linear model when all the data are included (equation 3.3.5.4) occurred in the 700 treatment in period 1 and was caused by a high per unit area estimate for Poa. The population density estimate for Poa in this treatment was higher in period 1 than period 2 (27450 vs 15450 $\pm$ 2687 units m^{-2}) and it was this high value that was primarily responsible for the high senescence value. If the population density of Poa had been lower and that of ryegrass higher in period 1, the per unit area estimate of senescence would have been reduced because senescence rates for individual ryegrass tillers was lower than that for Poa tillers (table 3.3.5.7).

For each growth model there was a unique net production function and for all three of the models there was a range of herbage mass over which 0.90 or more of maximum net production was achieved. This range for the rectangular hyperbola model was 850 - 1850 kg OM ha^{-1}, for the piece-wise linear model the range was 930 - 1360 kg OM ha^{-1} and for the logistic model the range was 800 - 1450 kg OM ha^{-1}. This result is consistent with the concept that net herbage production in mixed species swards is relatively constant over a range of herbage mass (Hodgson and Wade, 1978). Net production rate was relatively constant over these ranges of herbage mass because of compensating changes in growth and senescence.

Perhaps the most surprising aspect of the shape of these net production functions is the relatively low LAI value (2 - 4) associated with the range of herbage mass over which net production was relatively constant. In continuously grazed swards which have had time to adapt in morphological and population density terms, Hodgson et al (1981) have established from a range of experiments, including the one reported here, that maximum net production is likely to occur in the LAI range 3 - 4. This range is lower than the optimum LAI level of 5 suggested by both Davidson and Donald (1958) and Brougham (1958) for subterranean clover and perennial ryegrass respectively. However, these LAI = 5 values were derived from uninterrupted regrowth experiments and Hodgson et al (1981) make the point that the assumption that growth relationships within a sward are the same as those between swards has been too readily made. Hodgson et al (1981) demonstrated that at low LAI continuously grazed swards had higher canopy net photosynthesis levels than intermittently defoliated swards, this photosynthetic advantage declining as LAI increased. In low LAI swards there is less mutual shading of leaves

during expansion and therefore leaves have and retain high photosynthetic capacity (Leafe et al, 1978). Also, light interception can remain high in adapted low LAI swards (Hodgson et al, 1981). This adaptative process can be seen clearly in the canopy geometry data (section 3.3.6.2). As the mass of the sward decreased, the height of the ligule of the penultimate youngest grass lamina decreased more rapidly than the length of the pseudostem, with the consequence that tiller angle decreased from a value of approximately 60° in a sward of 2000 kg OM ha^{-1} mass to between 25 and 35°, depending upon species, in a 500 kg OM ha^{-1} sward. Foliage angle for ryegrass declined rapidly with decreasing herbage mass. Some of the ecological implications of Poa foliage angles were discussed earlier. Population density adaptation was discussed in the previous section (section 3.4.4) and the adaptation of individual plant units was discussed in section 3.4.3.

Increased frequency of defoliation is generally associated with reduced net herbage accumulation (Brougham, 1959 ; Jameson, 1963 ; Davidson, 1969) and contradictory results can probably be reconciled by consideration of defoliation height and utilisation (section 2.1). In this experiment, frequency of defoliation of both ryegrass and Poa tillers increased as herbage mass decreased. However net production, which in this experiment was equivalent to the net accumulation of green herbage that would have occurred had it not been consumed, did not decrease in a linear manner with decreasing herbage mass (figures 3.3.5.1 - 3.3.5.3) and at first increased to a maximum before decreasing. Growth rate decreased as frequency of defoliation increased

below a herbage mass of approximately 1000 kg OM ha^{-1} and this decline can be associated with reduced LAI (table 3.3.5.2). However, in this experiment there was a range of herbage mass over which differences in frequency of defoliation did not significantly alter net production rate. Hodgson and Wade (1978) found that frequency of defoliation had little effect on net herbage accumulation except where the defoliation interval was less than 14 days whereas the data from this experiment suggests a range (8 - 18 days) above and below which net production rate is reduced. Growth rate on the other hand was reduced when defoliation interval was approximately 8 - 10 days or less and intervals of defoliation greater than this had no effect on growth rate. The difficulties of interpreting the effects of defoliation frequency when only net herbage accumulation is measured are obvious. The effect of defoliation frequency on growth rate *per se* is the relationship that should be determined and as was stated earlier, it may be that below a critical defoliation interval reduced leaf area is the reason for reduced growth rate.

3.4.6 HERBAGE CONSUMPTION PER UNIT AREA

Consumption per hectare per day was briefly discussed earlier in section 3.4.2 with regard to the reliability of the tiller measurement technique. There was broad agreement between animal and sward estimates of consumption though the sward estimates were generally higher than the animal estimates. However, the assumption that NP = C = G - S (equation 3.1.2) was not met, consumption not being equal to net production, but if the lamina fraction only was

considered, then the assumption of equation 3.1.2 was met. Data from table 10 of appendix 3 were used to calculate lamina net production rates which were regressed against animal estimates of lamina consumption (500 treatment values adjusted for lamina from uprooted tillers). This regression was not significant but when lamina net production was estimated from regression models for lamina growth and senescence (table 10 B of appendix 3), the regression was significant ($R^2 = 0.70^{**}$) and the regression coefficient was not significantly different from unity (1.36 ± 0.37).

In period 1 the animal estimate of lamina consumption for the 1000 treatment was lower than that which would be expected if the estimates of growth and senescence were reasonable. The estimates of growth and senescence on this treatment conformed well to their respective models which suggests that in period 1 the 1000 treatment was understocked. Similarly in period 2 on the 1700 sward, the high lamina consumption measured can be taken to mean that this treatment was overstocked at that time. The fact that the 1700 treatment was overstocked in period 2 was recognised but the requirement to have a minimum number of animals with which to estimate intake with reasonable accuracy prevented any adjustment of stock numbers. The directly and indirectly estimated senescence values for the 1000 treatment in period 2 were very similar, which suggests that the sward estimates of consumption on this treatment were high (table 3.3.8.1).

It is difficult to resolve what the effects of changes in stocking density on consumption, growth and senescence might be. For example

the animal response to a higher stocking density might be to reduce daily intake or maybe to maintain daily intake by grazing longer. Similarly, the response to a lower stocking density might be to increase daily intake or maybe to maintain daily intake and reduce the time spent grazing. The results of this experiment suggest that it is more difficult to maintain NHA = 0 in swards of high mass and that small changes in stocking density can affect consumption and therefore senescence. Stocking density appeared to be less critical in the lower mass swards, small changes having little apparent effect on consumption and senescence.

3.4.7 INTAKE PER ANIMAL AND GRAZING BEHAVIOUR

Herbage intake for the ewes, whether expressed as total organic matter, green organic matter or green lamina organic matter, increased with herbage mass, and linear models fitted the data equally as well as the logistic models. Linear increases in the intake of wethers with increasing herbage mass have been reported (Hodgson and Milne, 1978) but the generally accepted model of intake is asymptotic (Hodgson, 1977). The herbage intakes of the lambs clearly reached an asymptote at 944 g OM $lamb^{-1}$ day^{-1} and logistic models for both the lamb and the combined ewe plus lamb intakes fitted the data better than linear models (tables 6 - 8 of appendix 3).

The mean total organic matter intake of the ewes on the 1700 treatment was 32 g OM kg LW^{-1} day^{-1} which compares well with a value

of 30 g OM kg LW^{-1} day^{-1}, extracted from the data presented by Maxwell, Doney, Milne, Peart, Russell, Sibbald, and MacDonald (1979), for Greyface ewes suckling single lambs at approximately the same stage of lactation. Maximum organic matter intake when the lambs were 10 - 15 weeks old was 26.1 g OM kg LW^{-1} day^{-1} and this too compares well with the level of 21.6 g OM kg LW^{-1} day^{-1} for single suckled lambs out of Greyface ewes reported by Maxwell et al (1979). However, perhaps the most interesting aspect of the ewe intake is the apparent treatment x period interaction. Intakes on the 1000 and 1700 treatment in period 2 were lower than those in period 1, whereas intakes on the 500 and 700 treatments were similar in both periods (figure 3.3.7.2). No treatment x period interaction was apparent in the lamb intake data.

The increase in the digestibility of the ewe's diet with increasing herbage mass (table 3.3.7.1) can be associated with the increase in the green lamina and the decreases in the pseudostem and dead tissue fractions of the diet that occurred as herbage mass increased (figure 3.3.7.3). On the 500 treatment and to a lesser extent on the 700 treatment, the ability of the ewes to select a highly digestible diet would almost certainly have been impaired by the proximity of the uppermost laminae in the canopy to the soil surface, the tips of the penultimate youngest laminae of both ryegrass and Poa being approximately 10 mm above the soil surface. In a sward as prostrate as that of the 500 treatment dead tissue, which is usually found mainly in the lower levels of the canopy, must have been located just above or in contact with the soil surface.

For the ewes to consume the high proportion of dead tissue measured in their diet on this treatment, they must have either ingested soil (Healy, 1967 ; Bircham, Crouchley and Aitken, 1981) and/or uprooted and consumed entire tillers to which dead tissue was attached. Both explanations are possible, and uprooting of ryegrass tillers did occur. This helps to explain the proportion of pseudostem in the diet of the ewes on the 500 treatment. Faecal ash proportion was significantly higher ($P < 0.01$) for the ewes on the 500 compared to the 1700 treatment (0.53 ± 0.01 vs 0.21 ± 0.04) which suggests that the proportion of soil in the diet of the 500 treatment ewes was greater than that of the 1700 treatment ewes. As with ewe intake data, there appears to be a treatment x period interaction in the green lamina fraction of the ewe's diet, the proportions for period 2 being lower than those for period 1 on the 1000 and 1700 treatments. The values for the 500 and 700 treatments were similar in both periods.

Intake per bite decreased with decreasing herbage mass and initially the ewes attempted to compensate by increasing the time they spent grazing but, as herbage mass decreased still further they no longer attempted to compensate and grazing time fell (figure 3.3.7.4). Dairy cows on tropical swards have been observed to react similarly but have also varied their rate of biting (Chacon and Stobbs, 1976). Grazing times for both cattle and sheep vary between 4.5 and 14.5 hours per 24 hours (Arnold, 1981) and the mean maximum time recorded in this experiment was 14.4 hours on the 1000 treatment in period 2.

Grazing time has normally been found to increase with decreasing herbage mass (Arnold, 1960 ; Allden and Whittaker, 1970 ; Hodgson and

Milne, 1978 ; Jamieson and Hodgson, 1979 a) but, with the exception of Allden and Whittaker (1970), levels of herbage mass have generally been 1000 kg OM ha^{-1} or more. In Allden and Whittaker's (1970) experiment 'A', grazing time increased rapidly with decreasing herbage mass below 1800 kg DM ha^{-1}, but above this level grazing time was constant. The lowest herbage mass measured was 500 kg DM ha^{-1}. However, if the Lolium rigidum Gaud. based pastures of experiment 'A' and the undisturbed L. rigidum of experiment 'B' were at all comparable, then the differences in grazing time between these experiments and the one reported here are perhaps reconcilable. In Allden and Whittaker's (1970) experiment 'B', undisturbed swards of approximately 800 kg DM ha^{-1} had extended tiller lengths (base of tiller to tip of longest extended leaf) of approximately 6 - 7 cm. It seems a reasonable assumption to suggest that the 500 kg DM ha^{-1} sward in their experiment 'A' had extended tiller lengths in the region of 4 - 5 cm. Ryegrass extended tiller lengths for the 500, 700 and 1000 treatments were 2.4, 2.9 and 3.7 cm respectively. Similarly, sward surface heights were 1.3, 1.9 and 3.7 cm respectively. Perhaps, everything else being equal, the inflexion point beyond which grazing time for sheep begins to decline is below 4 - 5 cm extended tiller length.

Hodgson (1977) proposed that the level of herbage intake achieved in any circumstance could be considered to be the resultant of different drives ; the drive to eat to satisfy requirements, the drive related to physical satiety, the drive related to grazing activity and the drive to do other things. When the level of herbage mass declined below 1000 kg OM ha^{-1} the balance of drives may have been such that the animal considered that the effort required to obtain

more herbage was too great when balanced against the gains of a higher intake and therefore the time spent grazing declined.

There appeared to be a treatment x period interaction in grazing behaviour just as there was in herbage intake and in diet botanical composition. Thus, grazing time on the 1000 and 1700 treatments was higher in period 2 than in period 1 and intake per bite was lower. Rate of biting did not differ significantly between treatments in period 1 but did differ significantly in period 2 (table 3.3.7.2). Compared to period 1 the main difference in period 2 was a higher rate of biting on the 1700 treatment. Clearly the ewes reacted differently to the 1000 and 1700 treatment swards in period 2 and the only major sward variable to exhibit a similar treatment x period interaction was lamina growth rate (figure 3.3.5.4). Total growth rates were similar in both periods but lamina growth rates were lower for the 1000 and 1700 treatments in period 2 (figure 3.3.5.4). Higher pseudostem and reproductive inflorescence growth rates made up the difference between total and lamina growth rates in these two treatments in period 2. Therefore, for herbage mass to remain constant, which was true in the 1000 but not the 1700 treatment (table 3.3.2.1), the proportion of lamina must have decreased and that of stem-inflorescence increased. If animals react primarily to the mass of lamina in the grazed horizon, as suggested by Stobbs (1973, 1975) and Hendricksen and Minson (1980), then a change in the spatial distribution and amount of lamina mass (i.e. a change in the structure of the sward), with consequent effect on grazing behaviour, botanical composition of the diet and ultimately herbage intake would explain the treatment x period interactions. Unfortunately the green lamina mass (figure

3.3.6.2) and canopy structure (figure 3.3.6.1) data relate to period 2 only. It seems likely that a treatment x period interaction, due to the stage of growth effect between the two periods just described, would have been evident in these data as well. The lamina versus total mass relationship in period 1 could reasonably be expected to be similar to that for period 2 (figure 3.3.6.2) but with a higher asymptote value. The proportion of stem in the higher mass swards could have been expected to be lower in period 1 than period 2.

As the proportion of stem in the canopy of the 1000 and 1700 treatments increased and the bulk density of the lamina in the grazed horizon decreased due to pseudostem and internode extension, the grazing animal might find it increasingly difficult to maintain intake per bite at the level it had been previously if it attempted to select the same diet as previously. The grazing animal could reasonably be expected to attempt to compensate for reduced intake per bite by increasing the time spent grazing and possibly by increasing the rate of biting also. Intake per bite decreased, grazing time increased on both the 1000 and 1700 treatments in period 2 relative to period 1, and the rate of biting on the 1700 treatment was higher in period 2 than period 1 (figure 3.3.7.4 and table 3.3.7.2). At the same time the proportion of lamina in the diet could be expected to fall and the proportion of stem and dead tissue in the diet increase if the grazing animal grazed further down into the canopy. These events too occurred on the 1000 and 1700 treatments in period 2 relative to period 1 (figure 3.3.7.3). If the grazing animal was unable or unwilling for whatever reason to

compensate completely for the change in structure of the sward, then reduced intake could be expected. Lower levels of herbage intake were observed on the 1000 and 1700 treatments in period 2 compared to period 1 (figure 3.3.7.2).

3.4.8 TISSUE FLOW AND UTILISATION EFFICIENCY

In this study, the influence of sward state on the flow of tissue in a continuously grazed sward has been demonstrated. Net production was relatively constant over a range of herbage mass due to a compensatory relationship between growth and senescence. The reasons for this compensatory relationship, however, have not been established and the question remains as to why senescence increases with increasing herbage mass.

The requirement of maintaining NHA = 0 meant that the treatment swards were maintained at approximately constant LAI. Hodgson et al (1981) state that:

> 'from first principles, the proportion of new leaf tissue which must be removed to maintain a given LAI decreases linearly from a value approaching 1.0 as LAI approaches zero, to a value approaching zero at maximum LAI'.

Senescence must increase as the level of maintained LAI increases because proportionally less and less can be harvested. This means a decline in utilisation efficiency as maintained LAI or herbage mass

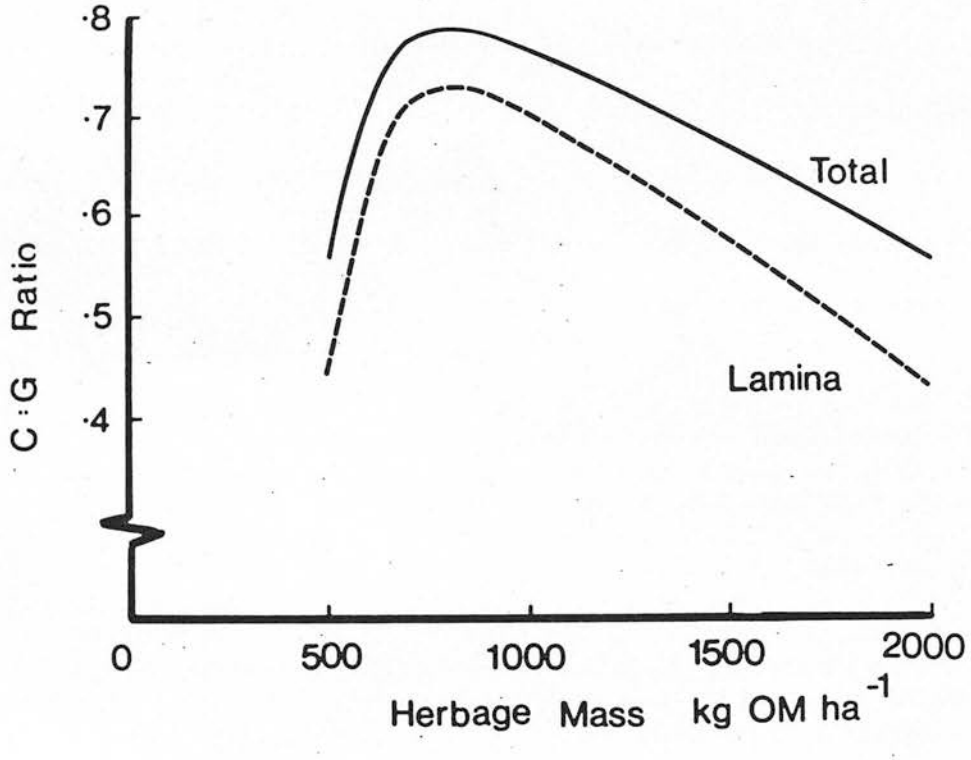

Figure 3.4.8.1 The relationships between utilisation efficiency (C : G) and herbage mass on total green and green lamina bases.

increases. In this experiment where NHA = 0 and NP = C = G - S (equation 3.1.2), C/G = 1 - S/G, and the C : G ratio is a measure of utilisation (harvesting) efficiency. This C : G index of utilisation efficiency was derived from the S : G ratio for both total green herbage (equation 3.3.5.3) and lamina (table 3.3.5.14, period 1 logistic model). Equation 3.3.5.5 was used to determine senescence. Utilisation efficiency as measured by the C : G ratio at first increased, reached a maximum at a herbage mass of approximately 800 kg OM ha^{-1}, and then declined with increasing herbage mass (figure 3.4.8.1). The decline in the C : G ratio at low ($<$700 kg OM ha^{-1}) herbage mass is due to the instability of the 500 treatment. The true C : G ratio for lamina only in this sward using animal consumption data would be approximately 1.4.

Further support for the argument that high levels of maintained herbage mass inevitably mean high senescence rates can be obtained from the rectangular hyperbola relationship between lamina mass and herbage mass (figure 3.3.6.2). If lamina mass does not increase with sward mass in a 1 : 1 manner, then the proportion of green lamina that can be harvested as maintained sward mass increases must decline if sufficient green leaf is to remain to maintain NHA = 0. Jackson (1974) found that swards cut to different heights effectively maintained similar levels of lamina mass at different heights above the ground, and data from Dr. J. King (pers. comm.) over the herbage mass range 2500 - 6100 kg DM ha^{-1} also yielded a non-linear relationship.

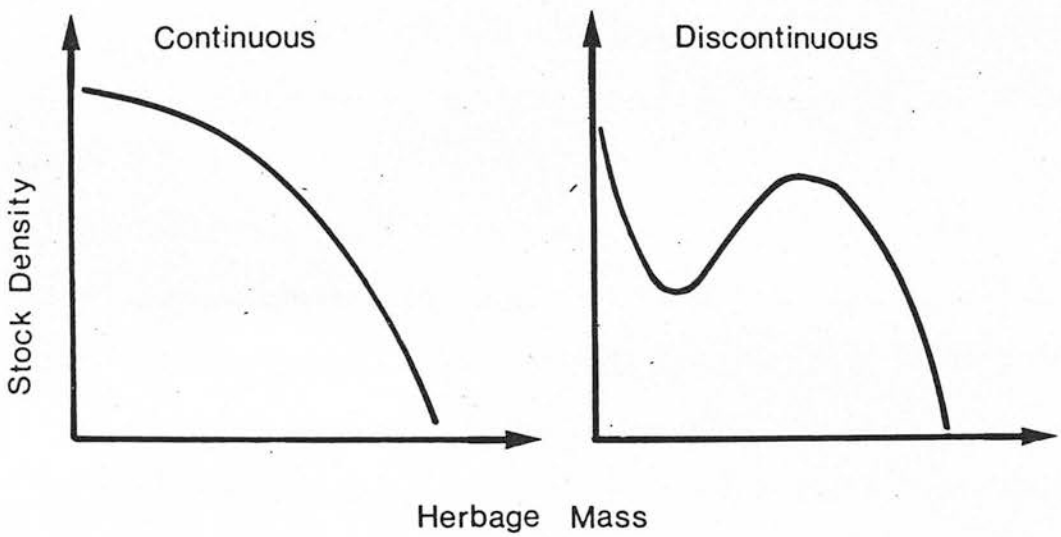

Figure 3.4.9.1 Isoclines of zero net herbage accumulation for continuous and discontinuous stability (After Noy-Meir, 1975).

High senescence rates, therefore, are an inevitable consequence of high levels of maintained herbage mass because utilisation efficiency must be low if the sward is to be maintained in steady state. Stocking density must therefore also decline in the manner depicted in figure 3.3.7.1.

3.4.9 STABILITY IN GRAZING SYSTEMS

Noy-Meir (1975, 1978$_a$) examined the theoretical stability of grazing systems using the basic assumption that rates of growth and intake depend only on green biomass, and came to the general conclusion that pastures may be continuously or discontinuously stable depending on the shape of the growth and intake functions. Examples of continuous and discontinuous stability are given in figure 3.4.9.1. The main condition for discontinuous stability is that the intake function approaches its maximum at a biomass lower than that at which the growth function approaches its maximum (Noy-Meir, 1978$_a$). In the study reported here, the pasture systems can be considered to be continuously stable as evidenced by the stocking rate versus herbage mass relationship (figure 3.3.7.1) which is also the isocline of zero net herbage accumulation, NHA = 0.

Noy-Meir (1975) has used what is in reality net production (growth - senescence) for his growth model based on a logistic model of net herbage accumulation over time during uninterrupted regrowth. There is at least one reason why this growth model is not appropiate to continuous stocking management systems. In a continuously stocked

sward net production is not the resultant of uninterrupted growth and senescence but is the resultant of growth and consumption such that only tissue that remains unharvested can senesce. All the tissue that grows is available to the grazing animal, not just the net production resultant, and the growth function has a shape that makes discontinuous stability impossible. Thus continuous stability is the only possibility.

The evidence for the possible existence of discontinuous stability in grazing systems (Noy-Meir, 1975) arises from comparisons of net production and intake functions from different experiments. In this experiment which was conducted on swards maintained in different states for a period of time, intake per animal unit approached its maximum value at a much higher herbage mass than growth (figures 3.3.5.3 and 3.3.7.2). Hodgson et al (1981) have demonstrated that swards can adapt in such a way that LAI does not have universal meaning because, for example, different age classes of leaf have different photosynthetic efficiency. Thus, particularly at low LAI, continuously stocked swards are likely to have higher growth rates than intermittently defoliated swards of the same LAI and conceivably the same herbage mass. To compare net production rates or even growth rates derived from uninterrupted regrowth data (Brougham, 1956 ; Davidson and Donald, 1958) with intake functions derived from studies on pasture availability (Allden, 1962 ; Willoughby, 1959) is invalid. Apart from the use of an inappropiate parameter, net production, Noy-Meir's (1975) analysis failed to recognise the impact of sward adaptation

on herbage production. The general absence, with the exception of Morley (1966), of reports in the literature of discontinuous stability is therefore not surprising.

3.4.10 IMPLICATIONS TO MANAGEMENT

This study has demonstrated that there is apparently little scope for increasing the net herbage production of continuously stocked temperate grasslands by management manipulation. There is, however, scope for the manipulation of individual and per unit area animal performance within the range of herbage mass over which the rates of net production change little. Lamb liveweight gain increased rapidly with herbage mass until 1000 kg OM ha^{-1} and thereafter more slowly, the rates of gain on the higher herbage mass treatments being similar to those reported by Maxwell et al (1979) for lambs from Greyface ewes. The per hectare liveweight gains using the actual stocking rates imposed were 3.1, 4.1, 4.0, and 4.5 kg LWG ha^{-1} day^{-1} on the 500, 700, 1000 and 1700 treatments respectively. However, in period 1 the 1000 treatment was understocked and in period 2 the 1700 treatment was overstocked, and if the stocking rates are estimated from the relationship depicted in figure 3.3.7.1, the corresponding levels of production were 3.1, 4.0, 5.8 and 3.4 kg LWG ha^{-1} day^{-1}. Clearly there is scope for the manager to achieve maximum per hectare performance or maximum individual performance within the range of herbage mass over which net production varies little. There is also scope for the manager to decide on the level of ewe performance to be achieved with future reproductive performance in mind.

3.4.11 CONCLUSIONS - EXPERIMENT 1

1. The tiller measurement technique has been demonstrated to provide useful estimates of tissue flow and to facilitate identification of the important components of herbage production. Thus herbage production responses to different managements can be due to changes in population density alone, to changes in individual plant unit growth processes alone, or to a combination of both.

2. In mixed species (perennial ryegrass - Poa annua - white clover) swards, the growth rates of individual tillers or stolons of the superior species (ryegrass and white clover) were correlated with their leaf areas. Shading reduced the growth rate of individual tillers of the inferior species (Poa annua).

3. Total and grass population densities were highest in the 700 kg OM ha^{-1} sward and fell as herbage mass both decreased and increased.

4. Population density and individual plant unit adaptation to management under continuous stocking resulted in compensatory changes in growth and senescence rates per unit area over a range of herbage mass such that net production rate per unit area was relatively constant over the range 800 - 1850 kg OM ha^{-1}.

5. Utilisation efficiency (ratio consumption : growth) increased to a maximum at a herbage mass of approximately 800 kg OM ha^{-1} and then declined as herbage mass increased. Senescence rate increased as herbage mass increased because lamina mass did not increase in a 1 : 1 manner with herbage mass. Therefore, for NHA = 0, proportionally less tissue could be harvested as herbage mass increased.

6. Green lamina was the principal component of the animal's diet. Changes in net lamina production rate were associated with changes in grazing behaviour, botanical composition of the diet and level of herbage intake of the grazing animal.

CHAPTER 4

EXPERIMENT 2

4.1 INTRODUCTION

Experiment 1 was conducted on continuously stocked swards, which with the exception of the 500 treatment, had adapted in terms of individual plant unit production rates and population density. Net production under these conditions was relatively constant over a range of herbage mass (0.9 of maximum net production achieved over the range 800 - 1800 kg OM ha^{-1} depending upon the model adopted) and leaf area index. However, it may be possible to obtain short term gains in net production by manipulation of herbage mass, for example, from low to high mass. The situation can be envisaged upon allowing a sward to grow from low to high mass whereby the growth rate of individual plant units is increased but because population density adaptation is less rapid, there may be short term gains in net production before the sward eventually adapts.

The concept examined in this experiment was that short term changes in net production may be possible because the elasticities of population density change and individual plant unit change (i.e. changes in growth and senescence rates) are different, population density changes being less rapid than changes in individual plant unit growth and senescence.

To evaluate the above concept, the 700 and 1700 treatment swards from experiment 1 were divided, one half of the 1700 sward grazed down to approximately the level of the 700 sward, and one half of the 700 sward allowed to grow to approximately the same

level as the 1700 sward. The techniques used in experiment 1 to measure tissue turnover were used to measure tissue turnover in these four swards in the autumn of 1979.

4.2 MATERIALS AND METHODS

The 700 and 1700 treatment swards from experiment 1 were maintained in as near steady state as possible by ewes alone after experiment 1 was completed. Nitrogenous fertiliser (N = 40 kg ha^{-1}) was applied to all paddocks on completion of experiment 1 and in mid-August a compound fertiliser was applied to all paddocks (N = 49 kg ha^{-1} ; P = 25 kg ha^{-1} ; K = 25 kg ha^{-1}).

All stock were removed from one half of the 700 kg OM ha^{-1} sward scheduled for change on the 20th August 1979, and the sward permitted to grow until a height approximately similar to that of the 1700 kg OM ha^{-1} sward was achieved. At the same time, additional stock were added to the half of the 1700 kg OM ha^{-1} sward scheduled for change and it was grazed down until a height approximately similar to that of the 700 kg OM ha^{-1} sward had been achieved. These changes were complete by the 13th September and all the swards were then maintained in as near steady state as possible by continuous but variable stocking with ewes throughout an intensive measurement period from 17th September until the 1st October when the experiment was completed. The layout of this experiment is depicted in figure 3.2.1.

The techniques used to measure herbage mass, sward surface

Table 4.3.1.1 Mean sward height (cm) and mean herbage mass (kg OM ha^{-1}).

Treatment	Herbage Height	Herbage Mass
LL	1.92 $\pm$ 0.14	838 $\pm$ 232
HH	5.03 $\pm$ 0.32	2157 $\pm$ 257
LH	6.28 $\pm$ 0.15	1994 $\pm$ 135
HL	1.90 $\pm$ 0.09	923 $\pm$ 91

height, species population density, individual tillers (stolons) and associated measurements for leaf area and weight conversions in experiment 1 were used in this experiment also. Herbage mass was not calibrated against sward surface height as in experiment 1, field measured values of herbage mass being used.

The individual tiller (stolon) data were handled in the way described in section 3.2.8 and statistically analysed by analysis of variance. The treatment x species interaction terms together with inflated LSD terms were used to compare treatments within species.

For the remainder of this chapter the 700 and 1700 kg OM ha^{-1} swards maintained throughout experiment 2 in their original state will be referred to as the LL and HH treatments respectively. The 700 kg OM ha^{-1} sward permitted to grow to approximately 1700 kg OM ha^{-1} will be referred to as the LH treatment and the 1700 kg OM ha^{-1} sward grazed down to approximately 700 kg OM ha^{-1} will be referred to as the HL treatment.

4.3 R E S U L T S

4.3.1 HERBAGE MASS AND HERBAGE HEIGHT

The LL and HL treatment levels of herbage mass were similar as were those of the HH and LH treatments. Sward surface heights in the LL and HL treatments were also similar but were different for the HH and LH treatments (table 4.3.1.1).

4.3.2 SPECIES POPULATION DENSITY

Ryegrass, Poa, white clover and total species population densities were highest in the LL treatment and lowest in the HL treatment (table 4.3.2.1). Total population density in the LH treatment was lower than in the LL treatment and greater than those in the HH and HL treatments which were not significantly different.

Table 4.3.2.1 Total and species population densities (units m^{-2})

Treatment	Ryegrass	Poa annua	White clover	Total
LL	35 517 a[1/]	21 750 a	4 217 a	63 783 a
HH	20 550 bc	5 617 b	1 017 a	29 483 c
LH	24 817 b	13 783 a	1 150 a	47 417 b
HL	14 483 c	4 033 b	917 a	23 850 c
SE	3 313	2 613	1 315	3 872

1/ Values in columns without common lower case letters are significantly ($P < 0.05$) different.

4.3.3 SPECIES PERFORMANCE

The definitions described in section 3.3.5 with regard to primary tillers and stolons are applicable to this section also.

Table 4.3.3.1 Leaf area per primary tiller (stolon) in mm^2.

Treatment	Ryegrass	Poa annua	White clover
LL	45 c	43 b	52 bc
HH	120 b	102 a	73 b
LH	184 a	125 a	208 a
HL	30 c	34 b	38 c
	SE = 9	LSD = 26	

Table 4.3.3.2 Leaf area index

Treatment	Ryegrass	Poa annua	White clover
LL	1.53 c	0.83 b	0.18 a
HH	2.32 b	0.48 bc	0.06 a
LH	4.57 a	1.71 a	0.19 a
HL	0.41 d	0.11 c	0.03 a
	SE = 0.14	LSD = 0.39	

4.3.3.1 SPECIES LEAF AREA PER PRIMARY TILLER (STOLON) AND LEAF AREA INDEX

Leaf area per primary tiller was higher in the HH and LH than the LL and HL treatments (table 4.3.3.1). Leaf area per primary clover stolon was highest in the LH and lowest in the HL treatment.

Leaf area index was highest in the LH and lowest in the HL treatment for both ryegrass and Poa, clover leaf area index was not significantly affected by treatment (table 4.3.3.2).

4.3.3.2 SPECIES PRIMARY TILLER (STOLON) PERFORMANCE

Lamina and total growth rates per primary tiller or stolon were highest for ryegrass followed by white clover and then Poa (table 4.3.3.3). There were no significant differences between the three species for pseudostem (stolon) or senescence rates per primary unit.

Table 4.3.3.3 Species primary tiller (stolon) performance in μg DM tiller (stolon)$^{-1}$ day^{-1}.

	Ryegrass	Poa annua	White clover	SE
Lamina growth	161 a[1/]	87 c	134 b	7.4
Pseudostem (stolon) growth	6 a	2 a	3 a	1.8
Total growth	167 a	89 c	136 b	7.8
Senescence	69 a	83 a	71 a	7.9

1/ In tables 4.3.3.3 and 4.3.3.7 values in rows without common lower case letters are significantly ($P < 0.05$) different.

Table 4.3.3.4 Lamina growth of primary tillers and stolons in μg DM tiller (stolon)$^{-1}$ day^{-1}.

Treatment	Ryegrass		Poa annua		White clover	
LL	111	b[1/]	54	c	95	b
HH	219	a	119	a	111	b
LH	209	a	107	ab	253	a
HL	105	b	68	bc	76	b

SE = 14.8 LSD = 42

Table 4.3.3.5 Total growth on primary tillers and stolons in μg DM tiller (stolon)$^{-1}$ day^{-1}.

Treatment	Ryegrass		Poa annua		White clover	
LL	121	b	61	c	96	b
HH	219	a	120	a	111	b
LH	224	a	107	ab	264	a
HL	105	b	68	bc	74	b

SE = 15.6 LSD = 45

Lamina and total growth rates per primary ryegrass tiller were similar in the HH and LH treatments and higher than in the LL and HL treatments (tables 4.3.3.4 and 4.3.3.5). The same generalisations apply to the Poa lamina and total growth rates. Clover lamina and total growth rates were higher in the LH treatment than in the other three treatments which were not significantly different to each other.

Senescence rates for ryegrass and clover primary units were highest in the LH treatment and lowest in the LL treatment (table 4.3.3.6). Poa primary tiller senescence rates were highest in the HH treatment.

Table 4.3.3.6 Lamina senescence of primary tillers and stolons in μg DM tiller (stolon)$^{-1}$ day^{-1}.

Treatment	Ryegrass		Poa annua		White clover	
LL	39	b	56	b	22	b
HH	78	ab	135	a	35	b
LH	114	a	69	b	179	a
HL	44	b	71	b	46	b

SE = 15.8 LSD = 45

1/ For tables 4.3.3.4 - 4.3.3.6 and tables 4.3.3.8 - 4.3.3.12 values in columns without common lower case letters are significantly ($P < 0.05$) different.

Pseudostem (stolon) growth rates and net production rates per primary tiller are detailed in tables 2 and 3 of appendix 5.

Table 4.3.3.8 Lamina growth per unit area in kg DM ha^{-1} day^{-1}.

Treatment	Ryegrass	Poa annua	White clover
LL	38.9 b	11.4 ab	3.5 a
HH	43.8 b	6.0 bc	1.1 a
LH	51.9 a	14.9 a	2.4 a
HL	15.1 c	2.6 c	0.7 a

SE = 2.5 LSD = 7.1

Table 4.3.3.9 Total growth per unit area in kg DM ha^{-1} day^{-1}

Treatment	Ryegrass	Poa annua	White clover
LL	42.4 b	12.7 a	3.6 a
HH	43.8 b	6.0 ab	1.1 a
LH	55.5 a	14.9 a	2.5 a
HL	15.1 c	2.6 b	0.7 a

SE = 2.6 LSD = 7.4

Table 4.3.3.10 Lamina senescence per unit area in kg DM ha^{-1} day^{-1}.

Treatment	Ryegrass	Poa annua	White clover
LL	12.8 b	10.6 a	0.8 a
HH	14.9 b	6.2 ab	0.3 a
LH	28.2 a	9.5 a	1.8 a
HL	5.9 c	2.2 b	0.3 a

SE = 2.2 LSD = 6.2

4.3.3.3 Species Per Unit Area Performance

Lamina, total growth and senescence rates per unit area were highest for ryegrass followed by Poa and then white clover (table 4.3.3.7). Net production rates for Poa and white clover were not significantly different and were lower than the rate for ryegrass.

Table 4.3.3.7 Species performance in kg DM ha^{-1} day^{-1}.

	Ryegrass	Poa annua	White clover	SEM
Lamina growth	37.4 a[1/]	8.8 b	1.9 c	1.2
Pseudostem (stolon) growth	1.8 a	0.3 b	0.1 b	0.3
Total growth	39.2 a	9.1 b	2.0 c	1.3
Senescence	15.5 a	7.1 b	0.8 c	1.1
Net production	23.7 a	2.0 b	1.2 b	1.7

Lamina, total growth and senescence rates per unit area for ryegrass were highest in the LH treatments, intermediate in the LL and HH treatments, and lowest in the HL treatment (tables 4.3.3.8 - 4.3.3.10). White clover per unit area lamina, total growth and senescence rates did not vary significantly with treatment. Poa lamina, total growth and senescence rates were higher in the LL and LH treatments than in the HH and HL treatments but not always significantly so. Pseudostem (stolon) growth rates per unit area are given in table 4 of appendix 5.

White clover and Poa per unit area net production rates did not vary significantly with treatment (table 4.3.3.11). Ryegrass per unit area net production rates were similar in the LL, HH and LH treatments and significantly higher than the rate in the HL treatment.

Table 4.3.3.11 Net production per unit area in kg DM ha^{-1} day^{-1}.

Treatment	Ryegrass	Poa annua	White clover
LL	29.6 a	2.1 a	2.8 a
HH	28.9 a	-0.1 a	0.8 a
LH	27.3 a	5.5 a	0.8 a
HL	9.2 b	0.4 a	0.4 a
SE = 3.5	LSD = 9.9		

The combined species (ryegrass + Poa + white clover) per unit area total growth, senescence and net production rates responded to treatment in a manner similar to that of ryegrass alone (table 4.3.3.12).

Table 4.3.3.12 Combined species, total growth, senescence and net production in kg DM ha^{-1} day^{-1}.

Treatment	Total Growth	Senescence	Net Production
LL	58.7 b[1/]	24.2 b	34.5 a
HH	50.9 b	21.6 b	29.3 a
LH	73.0 a	39.5 a	33.6 a
HL	19.0 c	8.2 c	10.8 b
SE =	4.6	3.8	6.2

4.4. D I S C U S S I O N

4.4.1 INTRODUCTION

Herbage mass and sward surface height in the 700 treatment of experiment 1 and the LL treatment of experiment 2 were similar, but height had decreased and mass increased in the HH treatment of experiment 2 compared to the 1700 treatment of experiment 1. Dead tissue probably accumulated in the 1700 sward during the season, resulting in higher mass at equivalent height in experiment 2. Also patchiness in the 1700 sward, with grazed and ungrazed portions, increased as the season progressed. This may have affected not only the amount of dead tissue in the sward but also the mean surface height of the sward. Fortunately the absolute values of sward surface height and herbage mass achieved did not affect the concept under examination, which was that short term changes in net herbage production can be induced by manipulation of herbage mass.

4.4.2 SPECIES PERFORMANCE

4.4.2.1 Species Primary Unit Performance

Lamina and total growth rates per primary unit were greater in ryegrass than in clover which contrasts with the results of experiment 1. White clover has a slightly higher temperature optimum than ryegrass (Mitchell, 1956) and the mean daily air temperature of the two measurement period in experiment 1 was 12.6°C compared to

1.1°C in experiment 2. Mean soil temperatures (5 cm) in experiment 2 was 9.6°C. As in experiment 1, the low primary tiller growth rates for Poa were probably associated with shading by ryegrass but the S : G ratios for Poa in all except the LH treatment were greater than unity which suggests that some Poa tillers were also dying. This was not surprising as the experiment was conducted at the end of the grazing season and Poa annua is predominantly an annual (Wells, 1974 a). The higher S : G ratios for clover in experiment 2 compared to experiment 1 may also reflect dying back on some stolons as temperatures fell towards the end of the grazing season.

Both ryegrass and Poa growth rates were highest in the higher mass swards (HH and LH) which can be associated with bigger tillers and greater leaf area per tiller (table 4.3.3.1) compared to the lower mass swards (LL and HL). However, clover growth rates per primary stolon were significantly lower in the HH than in the LH treatment. This difference can be attributed to the greater leaf area on the primary stolons in the LH treatment. In the HL treatment, the low primary growth rates may not have been due to low leaf area alone but also to reduced photosynthetic efficiency of old leaf tissue (Woledge, 1978).

Senescence rates per primary unit were highest in the LH treatment for ryegrass and white clover, but not Poa. The S : G ratios for the three species in this treatment were 0.51, 0.68 and 0.64 respectively for ryegrass, white clover and Poa compared to 0.35, 0.32 and 1.12 in the HH treatment. Higher rates of senescence could reasonably be expected in the LH treatment because of hastened

senescence and death during the adaptation process. This reasoning can be applied to both ryegrass and white clover and appears logical but Poa does not fit to the pattern. It is possible that laminae on Poa tillers were unable to assume their normal grazing escapist habit (i.e. low foliage angle etc.) due to the combination of high population density and high herbage mass. A process can be envisaged whereby ryegrass tiller angles increased in response to greater competition for light as herbage mass increased and, because the sward was so dense, the Poa laminae were obliged physically to assume the same foliage angle as ryegrass. Consequently, the Poa laminae would be more liable to defoliation than in a fully adapted sward and therefore senescence would be reduced. The shorter interval between successive defoliations for Poa in the LH than the HH treatment (7.9 ± 0.50 vs 12.6 ± 3.1 days) supports this contention.

4.4.2.2 Combined Species Per Unit Area Performance

The response of tissue turnover on individual tillers and stolons to change in herbage mass was rapid but population density changes were slower and the interaction between these different elasticities of change was reflected in the per unit area performance of the three species. For example, the total growth rate per unit area for Poa was lower in the HH than the LH treatment, although primary tiller total growth rates were similar, because of the big difference in population density. At the combined species level, the higher total growth rate in the LH compared to the LL treatment occurred because higher individual plant unit growth rates more

than offset the decline in population density with increasing mass, whereas the higher total growth rates in the LH compared to the HH, and in the LL compared to the HL treatments, were due primarily to differences in population density. The same reasoning can be applied to senescence rates except that the higher rates in the LH compared to the HH treatment were due to differences in both individual plant unit senescence rates and population density. The resultant net production rates in the LL, HH and LH treatments were similar because of the compensatory relationships between rates of growth and senescence. However, in the HL treatment where both growth and senescence rates were low, the rate of net production was significantly reduced.

Reduced pasture yields have been associated with reduced population densities by Brougham (1960) and Wade (1979). Both Hodgson and Wade (1978) and Hodgson et al (1981) have emphasised the need to maintain population density if pasture yields are to be maintained in the long term. Clearly, individual plant unit response to change in sward management was elastic and almost certainly reflected changes in individual unit leaf area. Population density, on the other hand, was elastic when a decrease in population density was required to reach the adapted state but inelastic when an increase in population density was required. If population density change is associated with change in radiation and light levels as suggested by Grant et al (1981), it is possible that population density increase may be more elastic before than after the summer solstice.

Table 4.4.3.1 Changes in sward parameters over time.

Experiment	Treatment	Herbage Mass (kg OM ha^{-1})	Leaf Area Ryegrass Primary Tillers (mm^2)	Combined Species LAI	Total Population Density (Units m^{-2})
1	700†	697	42	1.84	51 709
2	LL	838	45	2.54	63 783
1	1700†	1742	145	4.03	32 033
2	HH	2157	120	2.85	29 483

† Mean of both periods.

The concept upon which this experiment was based was only partially supported by the results. Thus, different elasticities of change for individual plant units and population density were demonstrated, but an increase in net production was not obtained because increased senescence counteracted increased growth rate.

4.4.3 THE CONCEPT OF STEADY STATE

The basic assumption upon which both experiments 1 and 2 were based was that swards were maintained in as near steady state as possible with reference to herbage mass. For herbage mass not to change, net herbage accumulation must be zero. However, the fact that net herbage accumulation is zero does not necessarily mean that the sward is in a steady state with regard to other parameters. For example, in experiment 1, the balance of growth between lamina and pseudostem changed between periods 1 and 2 (figure 3.3.5.4). Likewise in experiment 2, the LH sward was in a steady state with regard to herbage mass but population density was almost certainly changing rapidly.

The 700 and LL swards of experiments 1 and 2 were in herbage mass terms similar as were the 1700 and HH swards. However, both LAI and population density levels in the two pairs of swards changed over time (table 4.4.3.1). The increase in LAI that occurred in the 700 sward can be attributed to the change in population density which may have been a response to nitrogen application (Langer, 1963) after the completion of experiment 1.

Similarly, the decline in LAI in the 1700 sward can be attributed to the change in population density which may have been the sward response to declining light levels (Grant et al, 1981). Clearly steady state conditions as defined by a reference parameter do not mean that other parameters remain in a similar state over time. Also, created differences in a reference parameter do not necessarily mean that other parameters are different. For example, the herbage mass, leaf area per primary tiller and total population density levels of the LL and HH swards were very different but their LAI were similar (table 4.4.3.1). It was therefore not surprising that growth, senescence and net production rates per unit area were similar in these two swards (table 4.3.3.12), the same LAI being merely subtended at different heights above the soil surface (Jackson, 1974).

The concept of steady state in grazed swards is clearly relative only to the reference parameter chosen, other parameters may change considerably in response to prevailing environmental conditions. Therefore the steady state concept in sward management should be applied with due consideration to its limitations.

4.4.4. CONCLUSIONS - EXPERIMENT 2

1. Compensatory changes in growth and senescence rates in a sward permitted to grow from low to high mass meant that net production rate was similar to that of swards maintained at either low or high mass. A sward reduced from high to low mass had a lower net production rate than those maintained at either low or high mass.

2. Change in growth and senescence processes on individual tillers or stolons was elastic and reflected changes in leaf area. Population density change, however, was inelastic when an increase was required to reach the state of an adapted sward, but was elastic when a decline was required.

3. The concept of steady state in the study of tissue flow in grazed swards is useful but should be used with care because parameters other than the reference parameter for steady state may change over time.

CHAPTER 5

THE IMPLICATIONS OF SEASONAL VARIATION IN TISSUE FLOW : A SIMULATION EXERCISE

5.1 INTRODUCTION

In this study, a conceptual model of the sward-animal interface based upon the results from the field experiments was constructed and a deterministic simulation model developed from this concept of the sward-animal interface. The simulation model was, therefore, restricted to steady state conditions in the sward, conditions that rarely prevail in the real world. This limitation, however, does not preclude examination of the sward-animal interface and the likely outcome of using different precepts to describe this relationship.

With the exception of the pasture growth models described by Galbraith, Arnold and Carbon (1980) and Sibbald, Maxwell and Eadie (1979), pasture growth has been modelled using net production as the parameter of growth. It has already been observed that the 'growth' functions in Noy-Meir's (1975, 1976, 1978 a, b) models are in reality net production functions as are those of Vickery and Hedges (1972), Smith and Williams (1973) and Edelsten and Newton (1975). In a continuously stocked pastoral system, the pasture available to the grazing animal is the new tissue grown plus existing green (live) tissue. A net production function is singularly inappropriate in such conditions because it is the resultant of growth and senescence and only unharvested tissue can senesce.

Simulation models of grazing systems (Vickery and Hedges, 1972 ; Arnold and Campbell, 1972 ; Smith and Williams, 1973 ; Arnold, Carbon, Galbraith and Biddiscombe, 1974 ; Edelsten and Newton, 1975 ; Arnold

Campbell and Galbraith, 1977 ; Vera, Morris and Ling-Jung Koong, 1977 ; Sibbald et al, 1979) all utilise concepts of how the sward-animal interface operates to transfer herbage from the sward to the grazing animal. Potential intake is frequently calculated from a liveweight function (Vickery and Hedges, 1972) ; Arnold and Campbell, 1972 ; Edelsten and Newton, 1975 ; Arnold et al, 1977 ; Vera et al, 1977) which is then reduced according to the proportions and digestibilities of green and dead herbage available. Sibbald et al,(1979)determined intake from the digestibility of ingested herbage and reduced it when a certain body fat content and condition in the grazing animal was reached. Noy-Meir's (1975, 1976, 1978 a, b) deliberately simple models of the grazing system have already been briefly discussed (section 3.4.9).

The universality of herbage mass as a vector that can be used to describe most of the variables associated with the sward-animal interface was established in experiment 1 and in this context, the role of herbage mass can be likened to that of leaf area index in pasture growth. For pasture growth, the physical and physiological properties of plant communities can be combined into a single vector, leaf area index (Brown and Blaser, 1968) ; and for the sward-animal interface, the complex relationships between sward and animal can be mediated by a single vector also, herbage mass.

Herbage mass has been used to control management decisions in upland sheep systems (Eadie, 1981). However, the question remains as to whether herbage mass is a sufficiently reliable index of sward and animal performance upon which to base management decisions. For example, the use of herbage mass as the sole criterion in

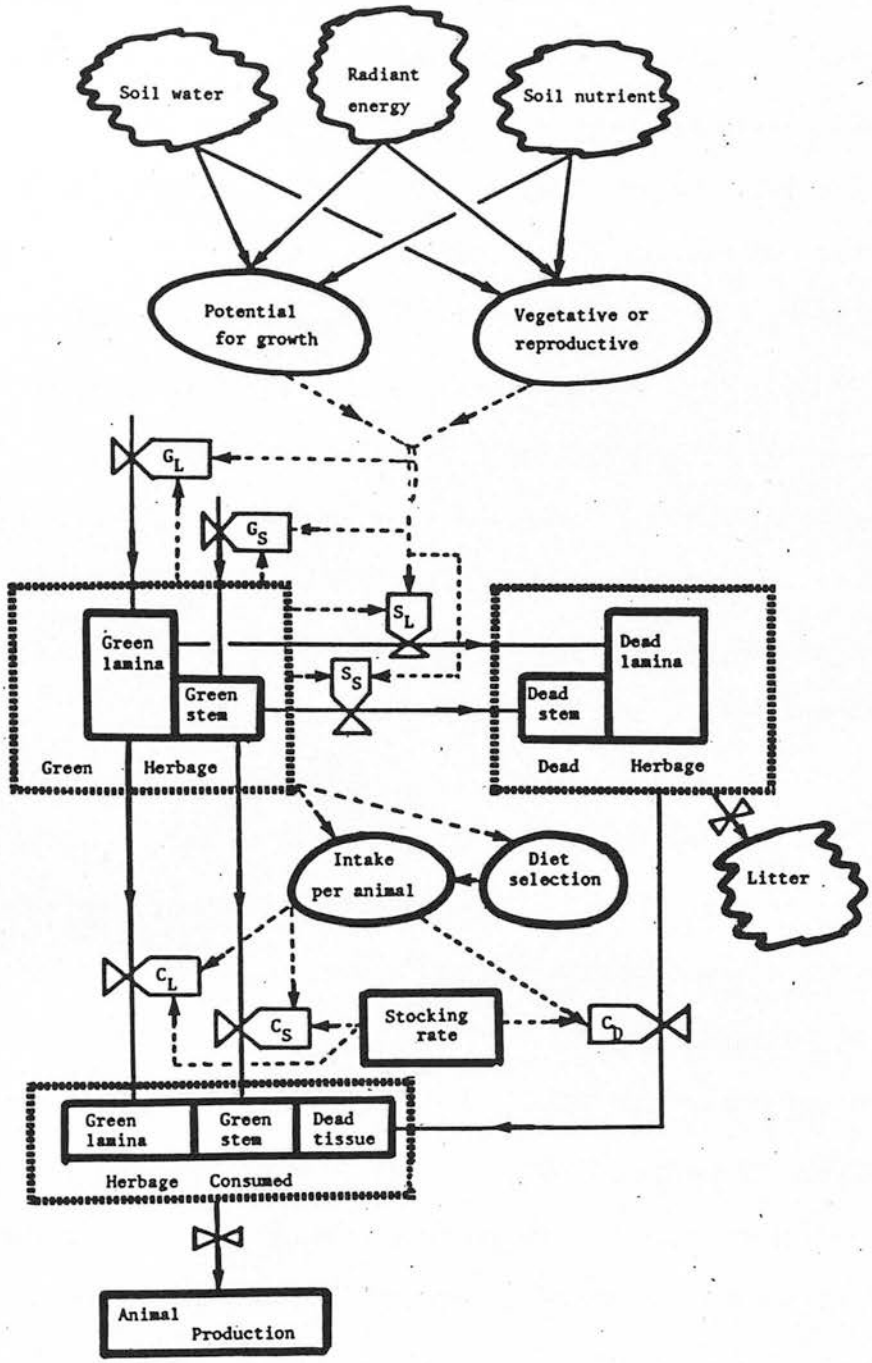

Figure 5.2.1 Conceptual model of the sward-animal interface based upon green herbage mass. The upper case letters G, S and C are shorthand for growth, senescence and consumption respectively. The L, S and D subscripts indicate the type of tissue, lamina, stem and dead respectively.

decision-making may be satisfactory in vegetative swards where growth is primarily lamina, but it is likely to be less satisfactory in reproductive swards where growth is partitioned between lamina and other tissue because the grazing animal reacts primarily to lamina (see chapter 3).

In the simulation exercise to be described, the usefulness of total green mass and green lamina mass as alternatives upon which decision-making could be based was examined by determining likely stocking rates under steady state conditions over the grazing season, based on either net herbage (lamina + stem) production or net lamina production. Net herbage production and net lamina production rates throughout the grazing season were obtained from simulated patterns of tissue flow.

5.2 CONCEPTUAL MODEL

The conceptual model of the sward-animal interface based upon green herbage mass is very simple. Green herbage mass rather than total herbage mass inclusive of the dead tissue component is a state variable, the level of which controls many of the rate processes (figure 5.2.1). Green herbage mass is used because herbage mass levels can vary between seasons (Campbell, 1964) solely because edaphic and climatic conditions favour either accumulation or disappearance of dead tissue. Green herbage is the photosynthetically active fraction of herbage mass (Leafe et al, 1978 ; Ong et al, 1978) and is also the fraction

of most interest to the grazing animal (Dudzinski and Arnold, 1973). Noy-Meir (1975, 1976, 1978 a, b) used green herbage mass in his analyses.

Climatic and edaphic factors are condensed into the auxiliary variable 'potential for growth' which, in conjunction with the level of green herbage mass, controls the rates of growth and senescence. Partitioning of growth and senescence into lamina and stem is controlled by the 'vegetative or reproductive' auxiliary variable.

Green herbage mass is used to control intake per animal and botanical composition of the diet through a further two auxiliary variables, which in conjunction with stocking rate determine consumption per unit area. Neither the live to dead nor leaf to stem ratios influence intake per animal.

This concept of the sward-animal interface divides herbage mass inclusive of the dead tissue fraction into green and dead lamina, and green and dead stem but only the total (lamina + stem) green herbage fraction has any influence on the rate processes. The green herbage mass concept of the sward-animal interface can probably only be applied to improved temperate swards where the live to dead ratio of herbage is maintained at relatively high levels throughout the grazing season and the accumulation of dead tissue does not influence either growth or herbage intake. In circu mstances where dead tissue is a major component of the sward, it is likely

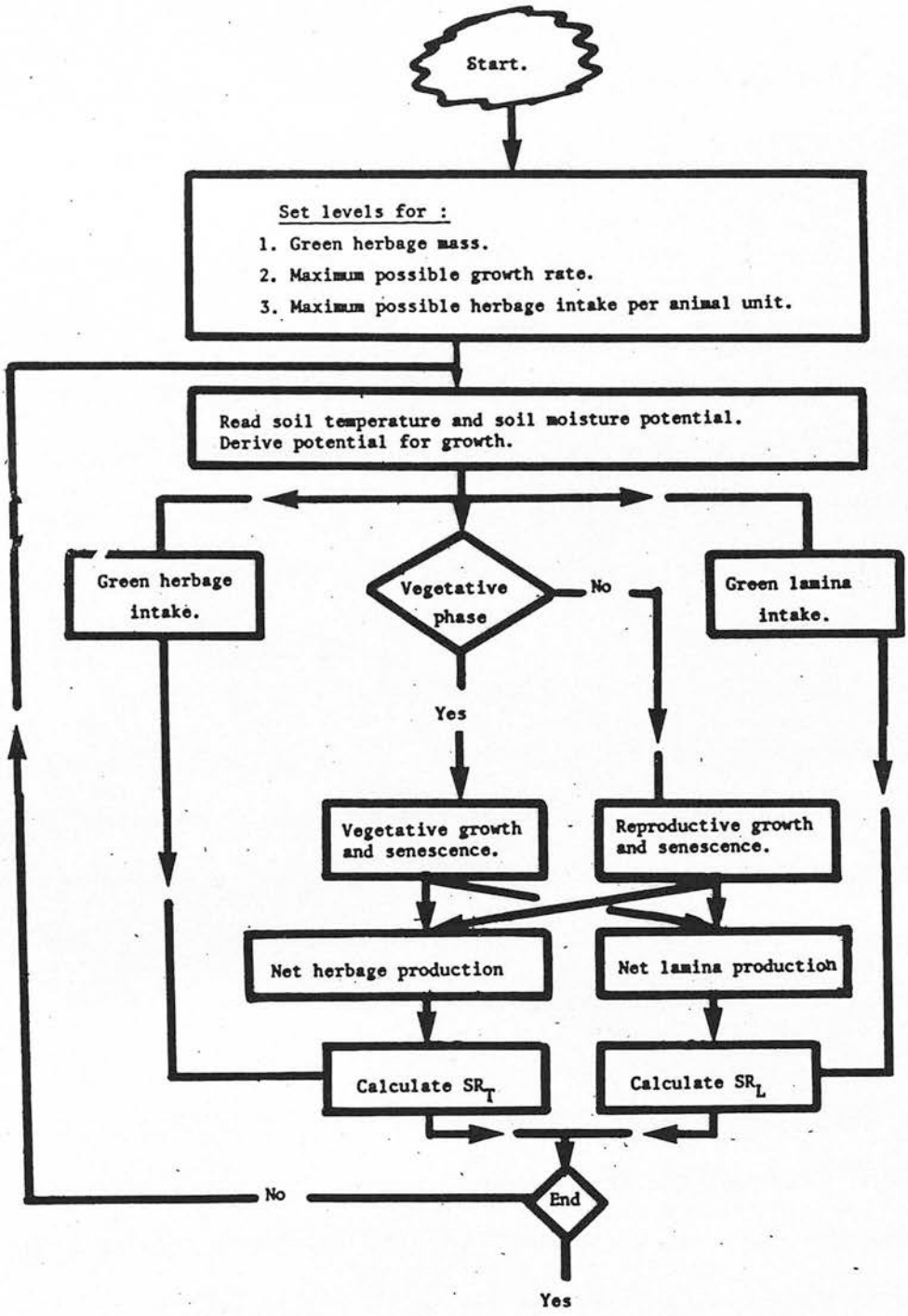

Figure 5.3.1 Flow diagram of simulation procedure.

that green herbage mass is of limited value as a vector describing the complex tissue flow mechanism in a grazed sward.

A conceptual model of the sward-animal interface could equally well be based upon lamina mass and would be identical to that depicted in figure 5.2.1 except that the rate processes would be influenced by green lamina mass rather than total green herbage mass. Such a concept would be subject to the same limitations as the total green herbage mass concept.

5.3 SIMULATION MODEL

A simulation model based upon the conceptual model (figure 5.2.1) was developed using green herbage mass as a state variable, the level of which controls many of the rate processes. The model assumes that swards are fully adapted and that they are maintained in as near steady state as possible by continuous but variable stocking. It was realised that the steady state concept has limitations, especially over time (section 4.4.3) but if this concept is adopted it is possible to derive consequential stocking rates by dividing net herbage production or net lamina production by the appropriate level of individual animal unit intake. A flow diagram (figure 5.3.1) illustrates the simulation procedure whereby stocking rates based upon net herbage production and net lamina production alone are derived. The time unit for simulation is one week and a source listing in Fortran is available from the author.

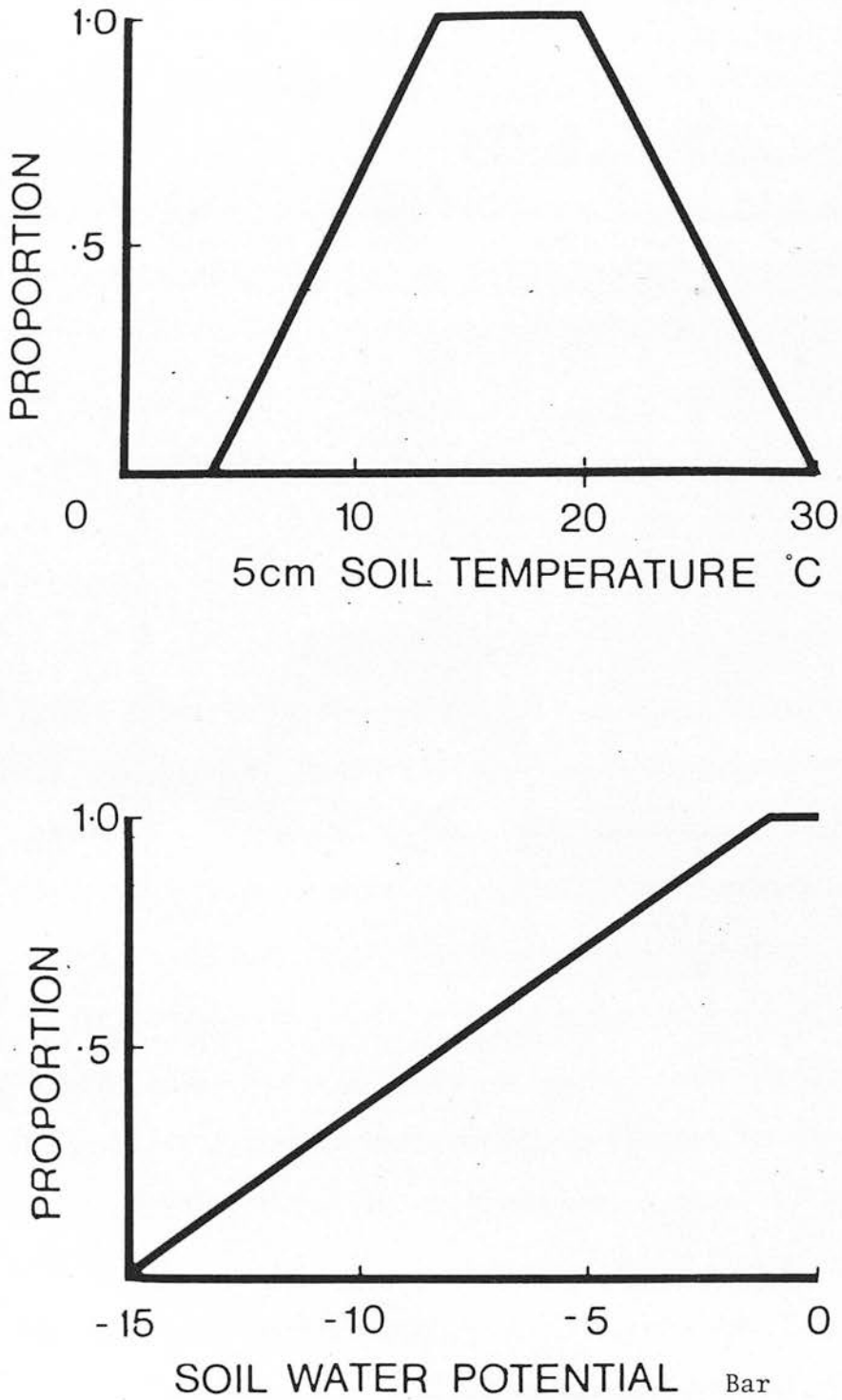

Figure 5.3.1.1 The influence of soil temperature (5 cm) and soil water potential on the potential for growth expressed as proportions of the maximum.

5.3.1 COMPONENT MODULES

5.3.1.1 Potential For Growth

To simulate growth throughout the grazing season, a potential-for-growth simulator was constructed. It must be emphasised that in no way are the rates of growth obtained intended to faithfully mimic rates of growth actually obtained in the field. The objectives of the growth simulator were to mimic patterns of growth throughout the grazing season and to be able to alter these patterns by changing the values of the driving variables. In this way the impact of climatic change on patterns of tissue flow could be examined.

Mean weekly values for 5 cm soil temperature and root zone soil water potential are the driving variables for the potential for growth simulator. A maximum possible growth rate when soil temperature, soil moisture and radiant energy are non-limiting is set for particular edaphic conditions, thus accounting for soil nutrient status. This maximum value is then reduced as soil temperature becomes limiting. The potential for growth is zero when the 5 cm soil temperature is 4°C and increases linearly to unity at 14°C. Between 14 and 20°C temperature is non-limiting but above 20°C temperature again limits growth, the potential for growth decreasing linearly to zero at 30°C (figure 5.3.1.1). Soil moisture does not limit growth until the soil water potential in the root zone is less than -2 bar, the potential for growth declining thereafter in a linear manner until zero is reached

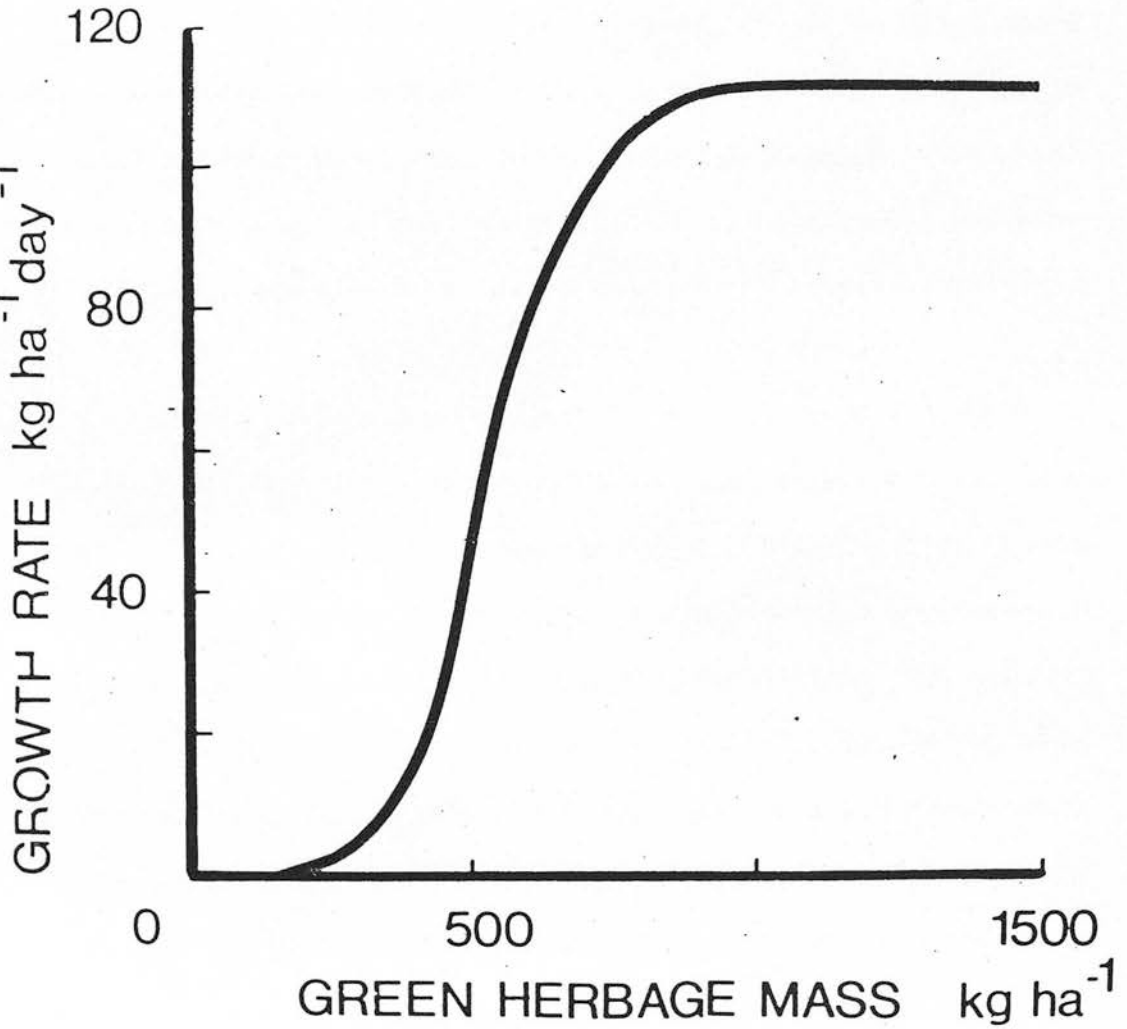

Figure 5.3.1.2 The relationship between growth rate and green herbage mass assuming an asymtpote value of 106 kg DM ha^{-1} day^{-1}

at -15 bar (figure 5.3.1.1). Vickery and Hedges (1972) used temperature dependent and soil moisture dependent potential growth functions. No growth occurred below 4°C soil temperature (4 cm), growth increased to a maximum at 22°C and declined to zero at 28°C. Vickery and Hedges (1972) used soil moisture in a similar manner to that in which soil water potential is used in this model. The rationale behind the soil water potential values chosen was that plant wilting occurs at approximately -15 bar and growth would therefore be limited at this point. The value of -2 bar above which soil water potential has no effect on growth is an arbitrary point which recognises that there is a range of soil water potentials approaching field capacity over which growth is not restricted.

5.3.1.2 Growth

Growth rate is calculated from green herbage mass using a logistic function for total growth calculated from experiment 1 data (figure 5.3.1.2). The asymptote value is not fixed but varies from the maximum possible when prevailing conditions are non-limiting to zero when temperature and/or soil water potential are limiting. Zero growth rate also occurs at a green herbage mass of 350 kg ha^{-1}.

Reproductive growth commences at a trigger temperature of 12°C at which time growth is partitioned between lamina and stem. This trigger temperature is arbitrary and is used merely as a means of creating seasonality. Also by making the trigger temperature less than that at which maximum growth rate is achieved, maximum

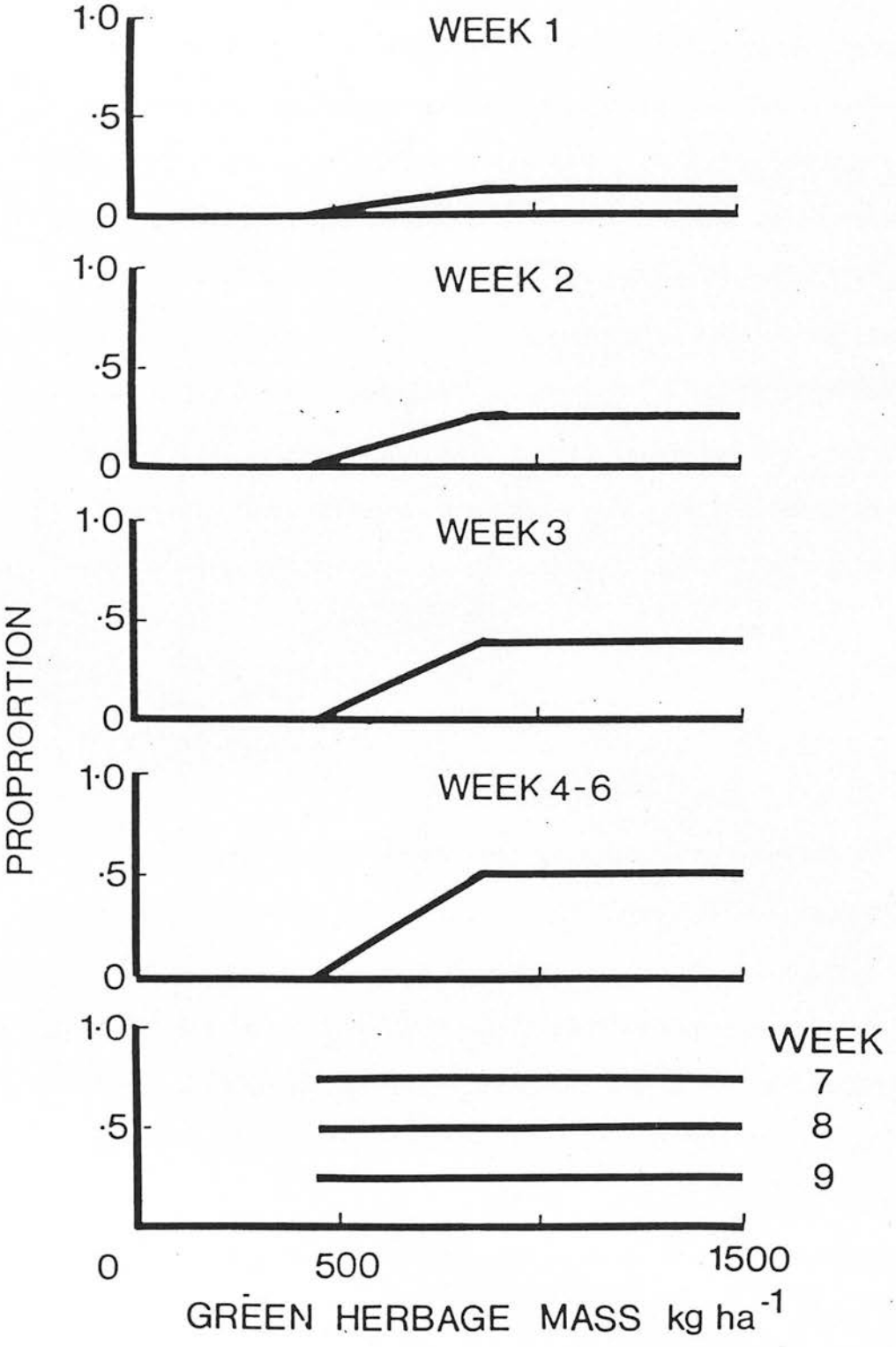

Figure 5.3.1.3 The relationship between stem growth rate, as a proportion of total growth rate for weeks 1 - 6 and as a proportion of maximum stem growth rate for weeks 7 - 9, and green herbage mass.

growth rate is achieved in the reproductive phase of growth. No stem growth occurs when green herbage mass is less than 450 kg ha^{-1}. Between green herbage levels of 450 and 800 kg ha^{-1}, the proportion of growth that is stem increases to a maximum which is maintained for levels of green herbage mass greater than 800 kg ha^{-1}. These levels were based on experiment 1 data. The proportion of growth per unit area channelled into stem growth increases to a maximum over a period of 4 weeks, is maintained at the maximum level for a further 2 weeks and then declines over a further 3 weeks after which all growth is vegetative. This decline in stem growth rate is achieved by reducing the maximum stem growth rate, achieved in weeks 4 - 6, by 0.25, 0.50 and 0.75 in the 7th, 8th and 9th weeks respectively of the reproductive phase of growth (figure 5.3.1.3). The 4 week period during which reproductive stem growth increases was based on experiment 1 data. The further 2 weeks of sustained reproductive stem growth followed by 3 weeks of declining growth are purely arbitrary but conform to the author's observations.

On cessation of the reproductive phase of growth, maximum growth rate is restricted to 0.60 of the temperature-dependent potential for growth when temperatures are 13°C or greater. By this means growth rate falls rapidly on completion of the reproductive phase of growth. A rapid fall in growth rate, of the order of 0.60 of the maximum growth rate achieved in the reproductive phase, has been reported by Brereton (1981). Also, at soil temperatures greater than 7°C and less than 13°C, the temperature-dependent potential

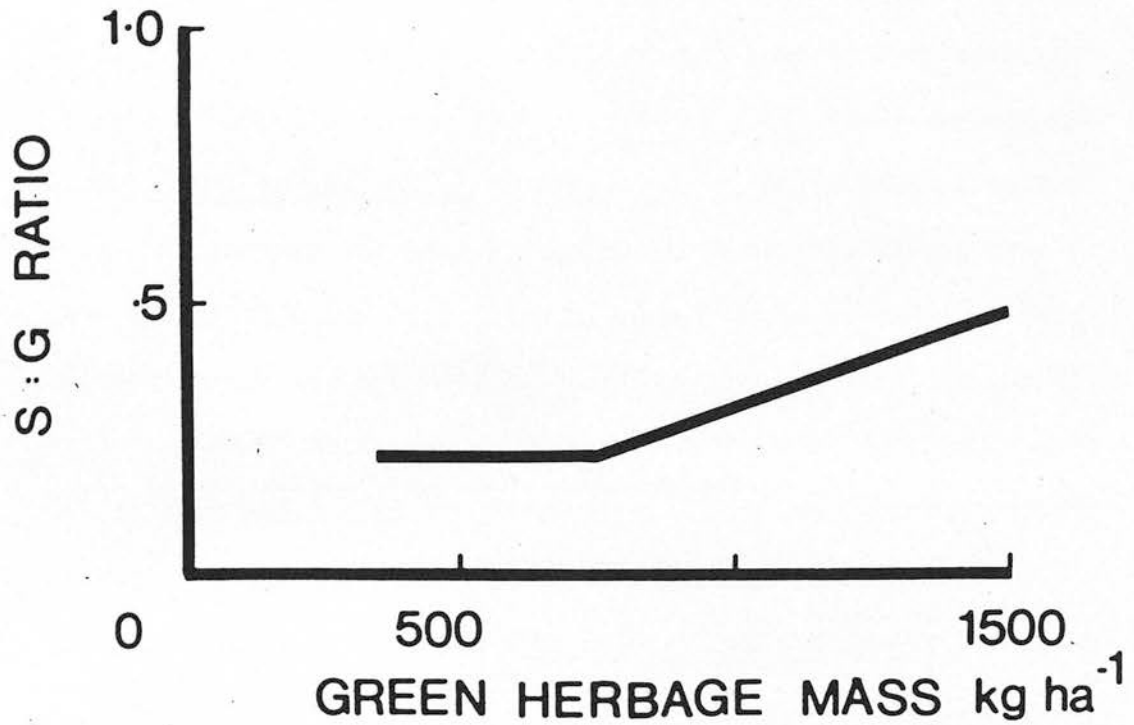

Figure 5.3.1.4 The relationship between S : G ratio and green herbage mass.

for growth is reduced by reducing soil temperature an arbitrary 2°C. This is done to allow simulation of the lag between radiant energy level and soil temperature decline as winter approaches.

Examples of the patterns of growth obtained from this simulation procedure are given in figure 5.5.1.

5.3.1.3 Senescence

The basic philosophy behind the construction of this module is that if tissue is not harvested by the grazing animal, it must senesce. The use of green herbage mass rather than herbage mass inclusive of dead tissue as the state variable means that unharvested reproductive tissue can be senesced over a finite period of time and transferred to the dead herbage state (figure 5.2.1).

Lamina senescence is calculated from green herbage mass and the prevailing total herbage growth rate. This is achieved by multiplying the total herbage growth rate by the S : G ratio appropriate to the current level of green herbage mass (figure 5.3.1.4). This relationship is based upon the logistic growth and linear senescence models from experiment 1, transformed to green herbage mass bases, for levels of green herbage mass greater than 750 kg ha^{-1}. Below this level the S : G ratio is constant (0.22), this level being approximately that of the 700 sward in experiment 1. The C : G ratio (figure 3.4.8.1), the inverse of

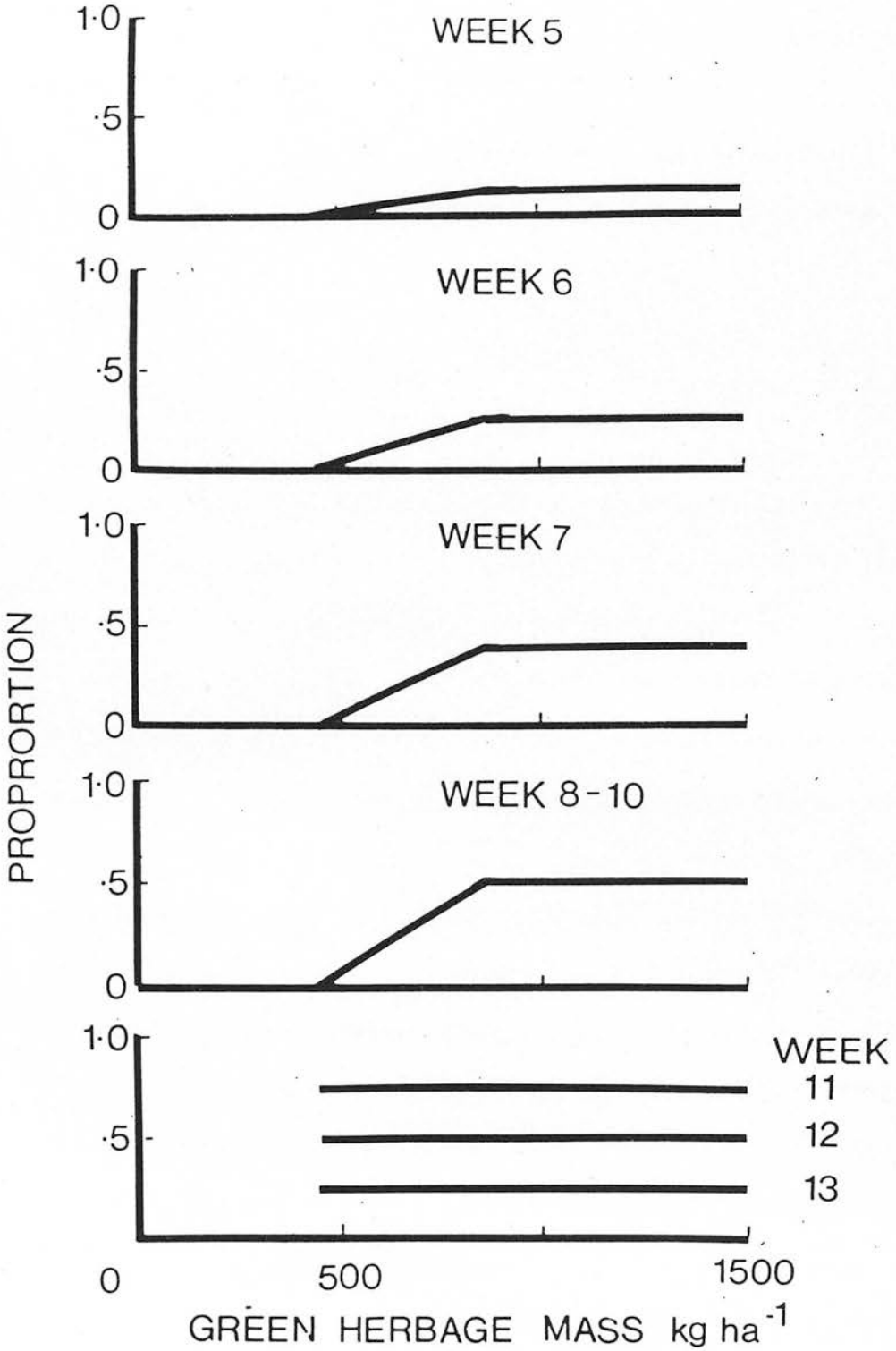

Figure 5.3.1.5 The relationship between stem senescence rate, as a proportion of growth rate for weeks 5 - 10 and as a proportion of maximum stem senescence rate for weeks 11 - 13, and green herbage mass.

the S : G ratio, decreased rapidly in experiment 1 below a herbage mass of approximately 800 kg ha^{-1}. This was considered (section 3.4.8) to reflect the instability of the 500 sward and a constant S : G ratio was thought to be a reasonable representation of the likely pattern below 750 kg ha^{-1}. This means that the grazing animal harvests a constant proportion of growth between green herbage mass levels of 350 and 750 kg ha^{-1}.

This approach to the determination of senescence is possible because the maintenance of steady state means that only a finite proportion of the herbage grown can be harvested (section 3.4.8), i.e. senescence is not determined by the voluntary intake of the grazing animal. It is based on two premises. (1) Lamina number per tiller is more or less constant during vegetative growth and therefore higher growth rates are associated with higher senescence rates, and (2) the S : G ratio describes the amount of tissue remaining after defoliation which must senesce. The relationship depicted in figure 5.3.1.4 is used for both the vegetative and reproductive phases of growth. Lower lamina growth rates during reproductive stem growth could possibly be expected to result in lower lamina senescence rates but experiment 1 data suggests that this is not so, presumably because lamina senescence relative to lamina growth increases because reproductive tillers senesce and die on completion of reproductive growth.

Reproductive stem tissue is programmed to senesce over a period of 9 weeks commencing in the 5th week of the reproductive

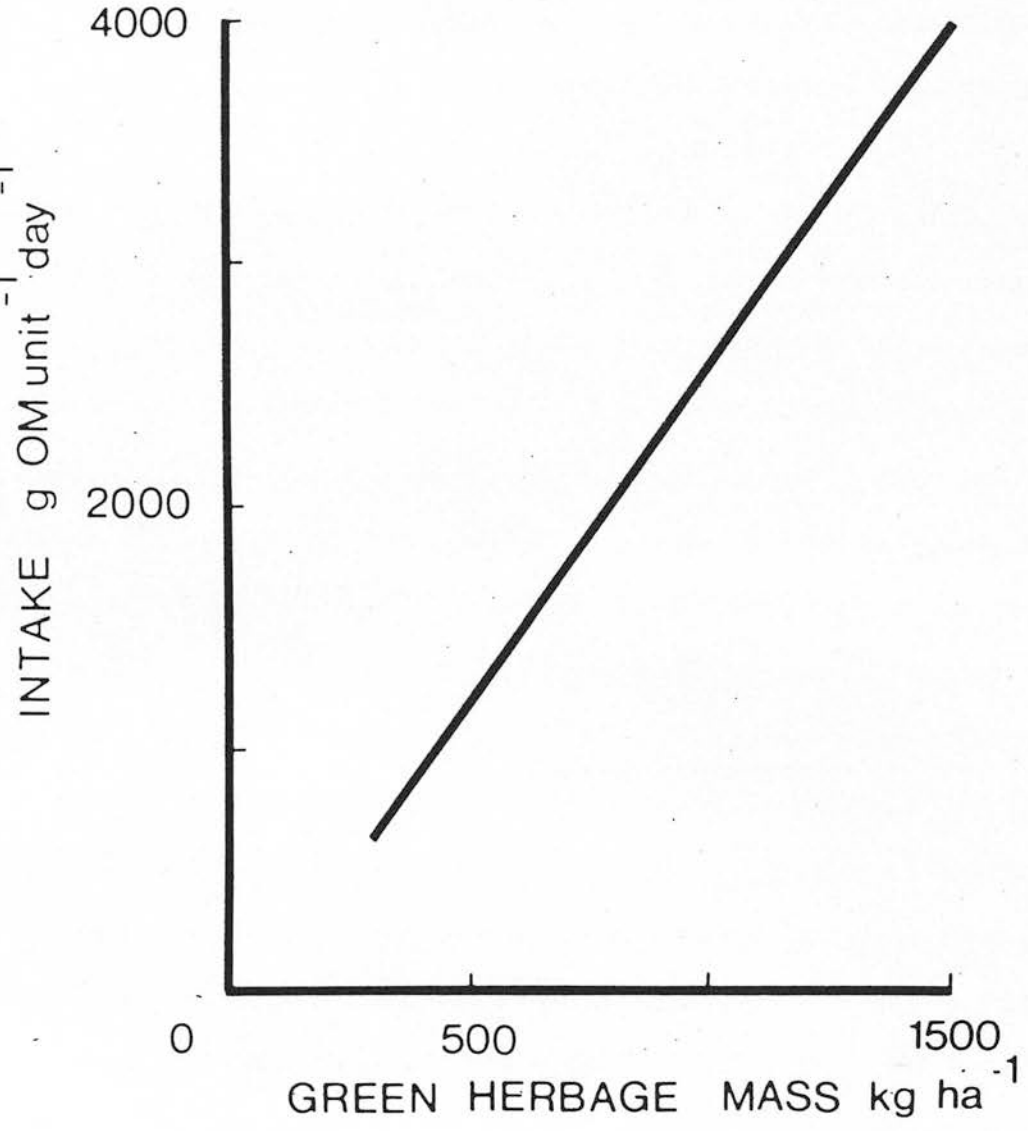

Figure 5.3.1.6 The relationship between organic matter intake per individual animal unit and green herbage mass.

phase. The proportion of stem tissue senescing increases to a peak between the 8th and 10th weeks of the reproductive phase and then declines to zero by the 14th week (figure 5.3.1.5). The basis of calculation is identical to that for stem growth and operates on the premise that tissue grown and not harvested must senesce. Grazing animals do ingest some stem tissue during the reproductive phase of growth and therefore the amount of stem senescing is reduced by the amount per unit area consumed. This is achieved by multiplying stem tissue intake per animal unit by the stocking rate determined from net lamina production for the period of reproductive tissue senescence only.

Examples of the patterns of senescence obtained using these procedures are given in figure 5.5.1.

5.3.1.4 Herbage Intake

This module calculates total organic matter intake from green herbage mass using a linear function derived from experiment 1 data for combined ewe plus lamb intake data (figure 5.3.1.6). Intake is set at zero at a green herbage mass of 350 kg ha^{-1} because growth rate is also zero at this mass. Maximum possible voluntary intake per animal unit is set for each run of the model and if the predicted intake (figure 5.3.1.6) exceeds this level, then the level used is the maximum possible voluntary intake. For example, the predicted intake per animal unit for a green herbage mass of 914 kg ha^{-1} is

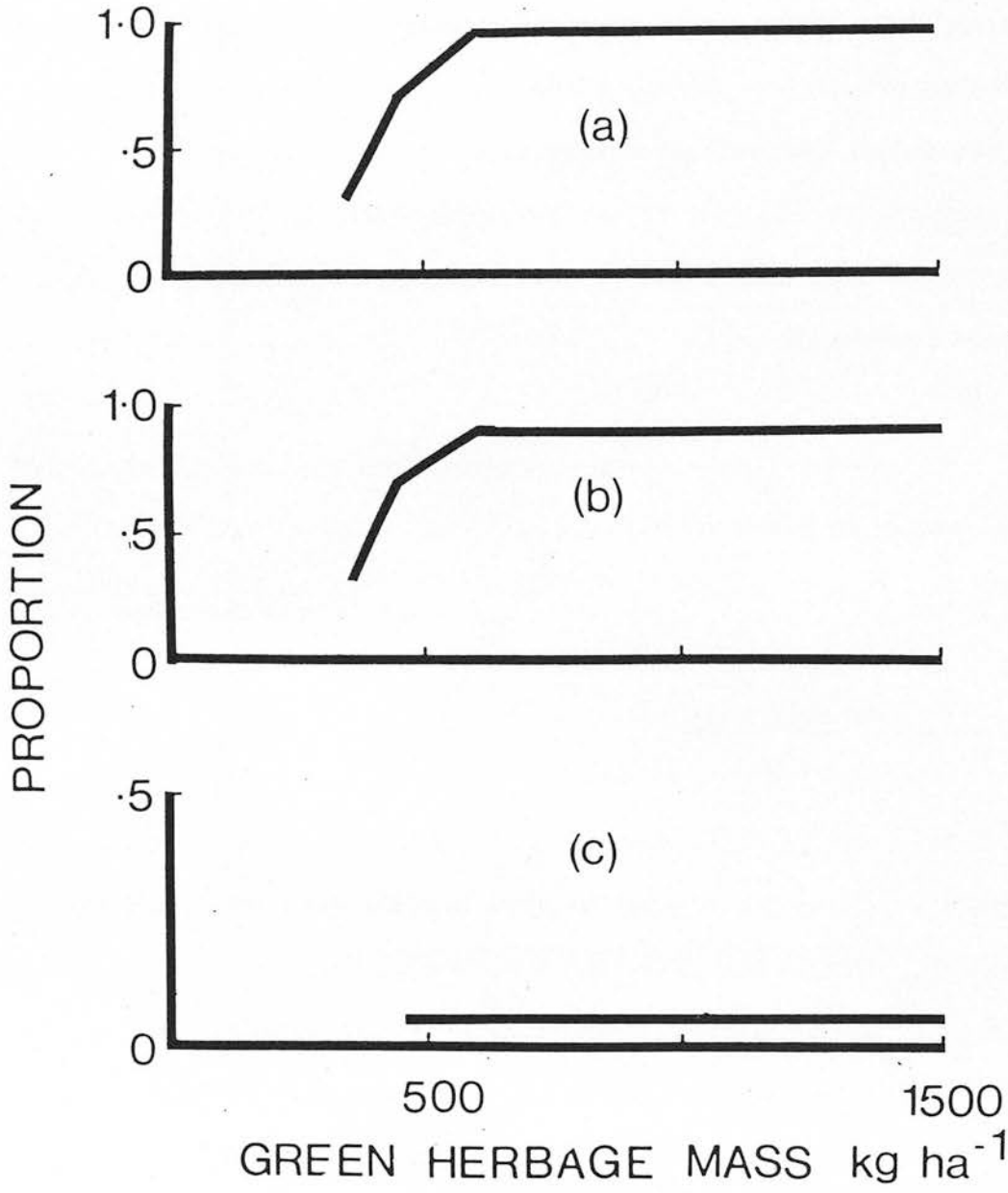

Figure 5.3.1.7 The relationships between the proportions of green lamina in the diet during vegetative growth (a) and reproductive growth (b), the proportion of green stem in the diet during reproductive growth (c), and green herbage mass.

2326 g OM day^{-1} but if the maximum possible voluntary intake was 2000 g OM day^{-1}, the latter value would be used.

During the vegetative phases of growth, total organic matter intake is partitioned between green lamina and dead tissue. The proportion of green lamina in the diet increases in a piece-wise linear manner from 0.3 at a green herbage mass of 351 kg ha^{-1} to 0.94 at a mass of 600 kg ha^{-1}, remaining constant thereafter. Dead tissue comprises the remainder of the diet. During the reproductive phase of growth and senescence, the maximum proportion of green lamina in the diet is 0.9 and for swards of green herbage mass greater than 450 kg ha^{-1}, the proportion of green stem in the diet is 0.06. The remainder of the diet is dead tissue. These relationships, all based on experiment 1 data, are depicted in figure 5.3.1.7.

5.4 OPERATION OF THE MODEL

The only data required to run the model besides mean weekly 5 cm soil temperature and root zone soil water potential, are the level of green herbage mass to be maintained, the maximum possible (asymptote) herbage growth rate for the particular environment and the maximum possible level of herbage intake per individual animal unit assuming that the availability of feed is non-limiting. Output from the model includes mean daily total herbage and lamina growth rates; total herbage and lamina senescence rates; total herbage and

lamina net production rates; mean daily intakes per animal unit of total herbage, green herbage and lamina; and mean daily stocking rates required to maintain steady state conditions based on either net herbage production or net lamina production.

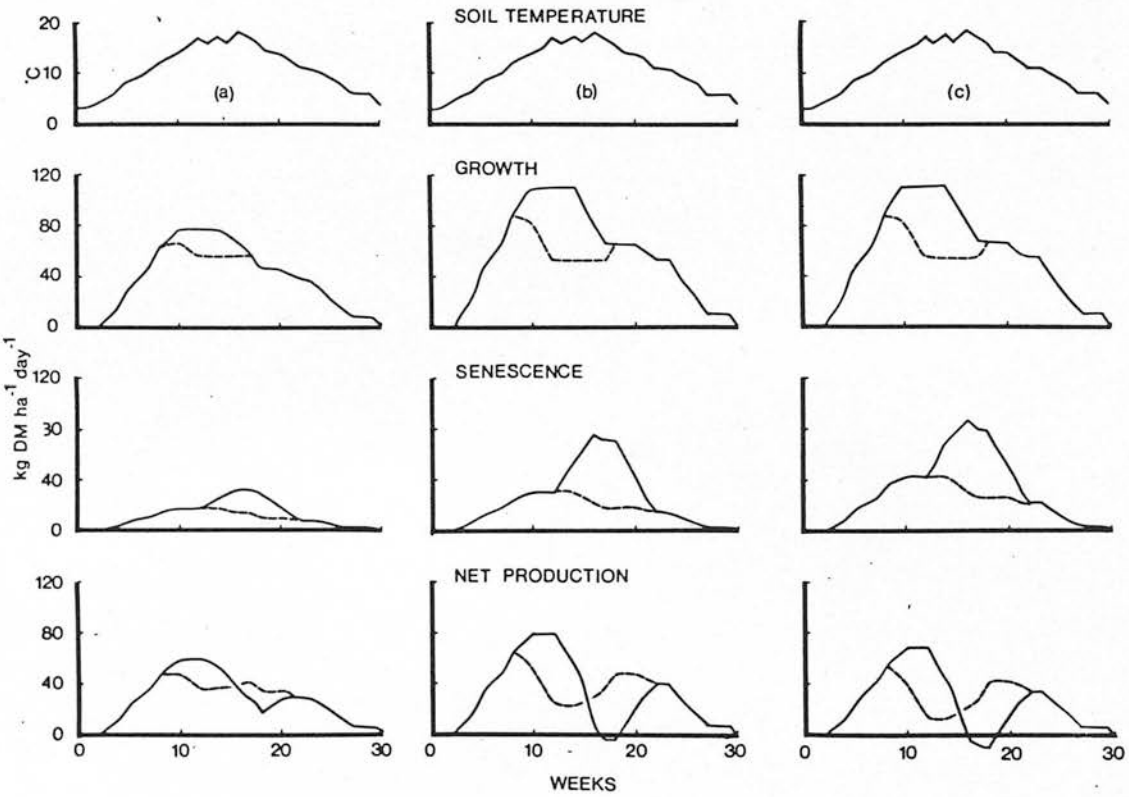

Figure 5.5.1 Soil temperatures from which rates of herbage (lamina + stem) and lamina growth, rates of herbage and lamina senescence, and rates of net herbage production and net lamina production were generated for three levels of maintained green herbage mass (a/ 584 kg ha^{-1}; b/ 914 kg ha^{-1}; c/ 1244 kg ha^{-1}) over a simulated grazing season of 30 weeks. Herbage (——), Lamina (-----).

5.5 RESULTS

Seasonal patterns of tissue flow for three levels of green herbage mass 584, 914 and 1244 kg ha^{-1}, assuming an asymptote growth rate of 110 kg DM ha^{-1} day^{-1}, are depicted in figure 5.5.1. These levels of green herbage mass would be equivalent to total herbage mass levels of 700, 1200 and 1700 kg OM ha^{-1} for experiment 1 swards. Mean weekly soil temperatures (5 cm) are also depicted in figure 5.5.1 and soil moisture is assumed to be non-limiting. For the remainder of the chapter, these three levels of green herbage mass will be referred to as Low (584 kg ha^{-1}), Medium (914 kg ha^{-1}) and High (1244 kg ha^{-1}).

Growth rates in the Medium and High swards were similar and higher than those in the Low sward. Reproductive tissue growth was greater in the Medium and High swards than in the Low sward and senescence rates increased as green herbage mass increased. Net herbage production and net lamina production rates reflected growth and senescence rates. Both in the Medium and High swards, two peaks of net herbage and net lamina production were evident whereas in the Low sward a single peak only was evident.

Stocking rates based upon net herbage production and net lamina production assuming steady state conditions for three levels of maximum possible voluntary herbage intake per animal unit, 1500 2500 and 3500 gm OM day^{-1} are depicted in figure 5.5.2. These levels of voluntary intake might correspond to a ewe carrying twins in late

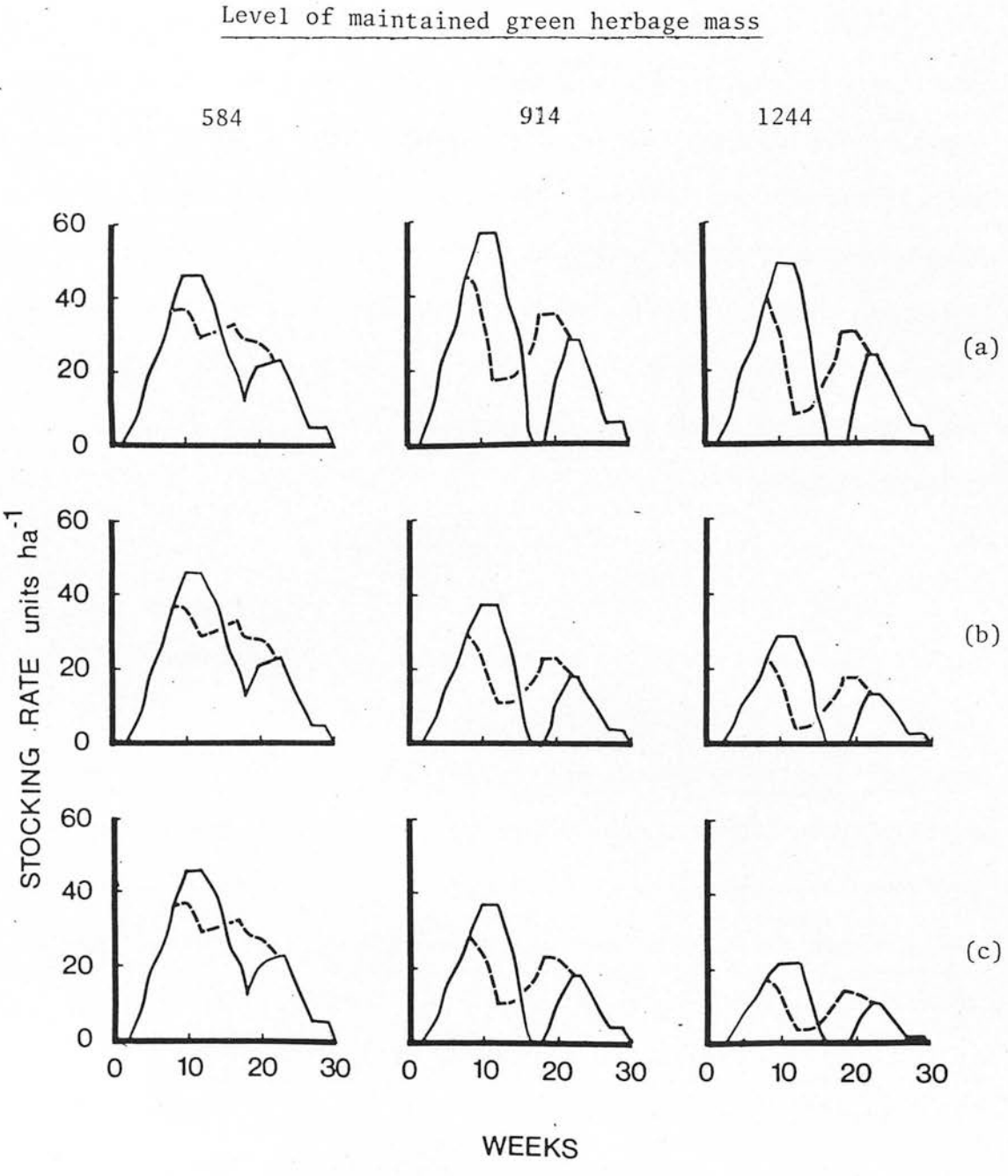

Figure 5.5.2 Stocking rates for three levels of maximum possible voluntary intake, 1500 g OM day^{-1} (a), 2500 kg OM day^{-1} (b) and 3500 g OM day^{-1} (c), at three levels of maintained green herbage mass over a simulated grazing season. Stocking rate based on net herbage production (——) and stocking rate based on net lamina production (-----).

pregnancy (1500 g OM day^{-1}), to a lactating ewe (2500 g OM day^{-1}) and to a lactating ewe plus lamb unit (3500 g OM day^{-1}). The actual levels of intake predicted for the Low, Medium and High swards assuming a maximum possible voluntary intake of 3500 g OM day^{-1} were 1419, 2326 and 3232 g OM animal $unit^{-1}$ day^{-1} respectively.

Stocking rates based on net herbage production were highest in the reproductive phase of growth and lowest during the period of reproductive tissue senescence. Stocking rates based on net lamina production were highest prior to commencement of reproductive growth, declined rapidly during reproductive growth and then rose again once the reproductive phase of growth was completed (figure 5.5.2).

5.6 VERIFICATION OF RESULTS

Verification of the model for the entire season is clearly impossible because the data on which the model is based were collected during three two week periods. However, some spot checks were possible for the Low and High swards because they were approximately equivalent to the 700 and 1700 kg OM ha^{-1} swards of experiment 1. Weeks 9 - 10, 12 - 13 and 23 - 24 corresponded approximately with periods 1 and 2 of experiment 1 and experiment 2 respectively.

Agreement between the levels of growth, senescence and stocking

Table 5.6.1 Comparison of simulated and experimental results.

	Total growth	Lamina growth	Lamina senescence	Stocking rate[2/]	Soil temperature (5 cm)
	kg DM ha^{-1}		day^{-1}	units ha^{-1}	°C
Weeks 9 - 10					
Low sward					
Model	73	65	16	37	13.5
Expt. data	79	58	41	39	14.7
High sward					
Model	105	84	42	16	13.5
Expt. data	105	81	47	13	14.7
Weeks 12 - 13[1/]					
Low sward					
Model	77	55	17	31	16.5
Expt. data	67	53	23	31	15.4
High sward					
Model	110	54	42	4	16.5
Expt. data	103	55	35	13	15.4
Weeks 23 - 24[3/]					
Low sward					
Model	35	35	7	21	10.5
Expt. data	59	59	24	64	9.6
High sward					
Model	50	50	19	23	10.5
Expt. data	51	51	22	20	9.6

1/ Assumes maximum possible intake per animal unit of 3500 g OM day^{-1}.

2/ Model levels based on net lamina production.

3/ Assumes maximum possible intake per animal unit of 1500 g OM day^{-1}.

rate predicted by the model and experimentally derived levels was generally good, but there were several exceptions (table 5.6.1). Model prediction of senescence for weeks 9 - 10 in the Low sward was much lower than the experimentally derived value (16 vs 41 kg DM ha^{-1} day^{-1}). A high estimate for Poa senescence in the 700 sward in period 1 (section 3.4.5.1) was the cause of this difference. Model prediction of stocking rate on the High sward in weeks 12 - 13 was much lower than the experimentally derived stocking rate (4 vs 13 animal units ha^{-1}) and this difference was due to the high numbers of stock retained on the 1700 treatment in period 2 so that reasonable estimates of herbage intake could be obtained (section 3.4.6).

The most serious discrepancy occurred in the Low sward in the 23 - 24 week period where predicted levels of growth, senescence and stocking rate were much lower than the experiment 2 results. However, the growth function of the model is based upon experiment 1 data when the mean LAI of the Low sward was 1.84 whereas in experiment 2 the LAI of this sward was 2.54 (table 4.4.3.1). Between a LAI of 1.8 and approximately 3.0 growth rate increases rapidly (figure 3.3.5.3) and a LAI of 2.5 would result in a growth rate much nearer the maximum possible. Because of the change in LAI of the Low sward over time it would be unreasonable to expect agreement between the levels predicted by the model and experimental data. The LAI of the High sward also changed over time, but this change had no effect because increasing LAI above 3.0 has no effect on growth rate (figure 3.3.5.3).

Within the limits of the available data, the spot verification checks suggest that the model predicts levels of the same order as the experimental data from which it was constructed.

5.7 D I S C U S S I O N

5.7.1 MODEL OUTPUT

The simulation model described is simplistic in every sense and no attempt has been made to simulate beyond a level which indicates likely patterns of tissue flow and consequent possible stocking rates. Some of the relationships used are empirical in the extreme. For example, the periods of time over which both reproductive growth and senescence increase and then decline are purely notional. In reality these periods of time may be longer or shorter depending upon season. Also the relationships between diet content and vegetative and reproductive growth are purely notional and are unlikely to be absolutely true. The dominance of green lamina in the diet is supported by experiment 1 data and evidence in the literature (Arnold, 1964) but pseudostem tissue, admittedly a small proportion, would also be present in the diet during the vegetative phases. The assumption that there is no pseudostem in the diet during the vegetative phases of growth makes the construction of the model much simpler because there is no need to simulate the pseudostem growth necessary to maintain steady state conditions. Provided that green herbage mass levels

are greater than 600 kg ha^{-1}, the errors associated with this assumption are likely to be small.

It is worthy of note that patterns of tissue flow for levels of green herbage mass below 550 kg ha^{-1} (650 kg OM ha^{-1} for experiment 1 swards) may be inaccurate because the experiment 1 data on which the model is based is not as reliable at very low levels of mass (section 3.4.2). Therefore use of the model should be restricted to levels of green herbage mass greater than 550 kg ha^{-1}.

Total herbage growth rate had a single peak in all three simulated swards whereas net herbage production had two peaks in the two higher mass swards, a phenomenon observed for net herbage accumulation by Anslow and Green (1967) in the United Kingdom and Baars (1976) in New Zealand. However, it is difficult to compare net herbage production and total net herbage accumulation because the former measures the accumulation of live tissue only whereas the latter includes dead tissue. The primary cause of the two peaks in net herbage production is the senescence of unharvested reproductive stem which at times is sufficiently high to result in negative rates of net herbage production. Zero levels of net herbage accumulation in mid-season can occur (Baars, 1976) but negative values are rarely recorded, although they are possible. However, high senescence rates are not necessarily associated with high disappearance rates for dead tissue, dead tissue could accumulate to disappear later, and on this basis negative net herbage production rates are quite feasible.

Perhaps the most important aspect of tissue flow illustrated in figure 5.5.1 is that net lamina production does not vary as much as net herbage production over the grazing season. It is clear from figure 5.5.2 that if stocking rate was based on net herbage production rather than net lamina production, then very high stocking rates would be required during reproductive stem growth followed by low or even zero stocking rates during reproductive stem senescence if the swards were to be maintained in steady state. However, because the grazing animal selects predominantly lamina, stocking to net herbage production would result in swards being overstocked during reproductive growth and understocked during reproductive tissue senescence. For this reason net herbage production would be an unsatisfactory index upon which to base decisions on stocking rate during the reproductive phase of growth. During vegetative phases of growth when net herbage production and net lamina production are virtually the same, both would be equally satisfactory indices upon which to base decisions on stocking rate.

Eadie (1981) argued that herbage mass or some derivative of herbage mass could be used as the basis of management decisions in upland sheep systems. There are dangers associated with basing management decisions on levels of sward herbage mass which in some circumstances may include high levels of dead tissue and in other circumstances low levels of dead tissue. For example, animal performance on a sward with a high dead tissue content could be less than that on a sward of the same mass but with a lower dead

tissue content due to differences in digestibility. A further problem that applies equally to the use of green herbage mass as the basis for decision making is that different decision rules would be necessary for vegetative and reproductive phases of growth. For example, similar levels of mass in vegetative and reproductive swards, if stocked at the same level, would result in lower effective (lamina) herbage allowance in the reproductive sward because of animal preference for lamina. A higher total herbage allowance would be required in the reproductive sward for the same effective herbage allowance. Apparently anomalous results from grazing experiments where animal performance has been poorer than expected despite high levels of total herbage allowance may be explicable in terms of effective (lamina) herbage allowance. Differences in levels of intake in spring and autumn (Jamieson and Hodgson, 1979 b) adds a further complication.

It will be clear from the foregoing discussion that if green herbage mass and net herbage production are to be used as the indices by which management decisions are controlled, then for a particular decision, the levels of these indices must change with the different phases of vegetative and reproductive growth. On the other hand, single levels of lamina mass and net lamina production could be used irrespective of the phases of vegetative and reproductive growth and therefore a lamina based index is likely to be more useful than herbage mass or even green herbage mass as a basis for making management decisions.

5.7.2 IMPLICATIONS TO MANAGEMENT

The most serious limitation of the simulation model described is its limited applicability to real world management systems because it is based upon the maintenance of steady state conditions. However, it is possible to extrapolate to a limited degree and discuss some of the implications of the results generated by the simulation model to the real world where stock numbers are usually fixed.

In some farming systems high levels of individual animal performance are required and this requirement can only be met by high levels of intake (e.g. in the vicinity of 3500 g OM animal unit^{-1} day^{-1} for a lactating ewe and lamb) which under continuous stocking can only be achieved at high levels of green herbage mass. The cost of this requirement for high levels of intake is the wastage of potentially harvestable herbage that must occur if the sward is to be maintained at a high mass. Estimated annual net lamina production assuming steady state conditions for the simulated Low, Medium and High swards were 5558, 6185 and 4930 kg DM ha^{-1} respectively assuming a 30 week grazing season with 3 weeks of zero growth due to low temperatures. To be able to utilise the high net lamina production of the Medium sward, intake per animal unit would have to be restricted to approximately 2300 g OM day^{-1} but the higher stock numbers that can be carried on this sward compared to the High sward could be expected to result in greater lamb liveweight gain per hectare (section 3.4.10).

The objective of some grazing management policies is to graze swards heavily early in the season to maintain the sward in a leafy state and to minimise future reproductive growth. Such a policy can perhaps be represented by the Low sward. Intake per lactating ewe plus lamb would be severely restricted on such a sward (figure 5.6.2) and both liveweight gain per individual lamb and per hectare (figure 3.3.7.6 and section 3.4.10) would be lower than levels in the Medium sward. Ewe liveweight loss would almost certainly occur (figure 3.3.7.6). Estimates of net lamina production over the first 18 weeks of the simulated grazing season, at which time reproductive growth is complete, for the Low and Medium swards were similar (4018 vs 3983 kg DM ha^{-1}). Therefore, there is little to be gained from hard grazing early in the season to control subsequent reproductive stem growth. In fact there may be severe penalties in individual animal performance terms (figure 3.3.7.6).

Conventionally, most grazing managers have a fixed number of stock. Early in the season, swards are likely to be hard grazed and maintained at a level approaching that of the low sward, but as the season progresses and grazing pressure is reduced, the swards increase in mass. If swards are allowed to reach levels of herbage mass approaching that of the high sward where net lamina production is low due to high senescence, the loss of potential feed is high. Subsequently, as growth slows, the mass of these swards is reduced as the grazing animal is obliged to eat into them. In many instances the sward is eventually reduced

to levels of herbage mass approaching that of the Low sward. If a 30 week grazing season with three weeks of zero growth is assumed as before and the following sequence is also assumed: weeks 1 - 7 Low mass sward; weeks 8 - 11 Medium mass sward; weeks 12 - 18 High mass sward; weeks 19 - 23 Medium mass sward; and weeks 24 - 30 Low mass sward; then lamina net production using the simulated data of figure 5.5.1 would be 5294 kg DM ha^{-1}. The lamina net production of both the maintained Low and Medium swards for the same period would be greater than this, 5558 and 6185 respectively. Such an analysis must be used carefully because of the many assumptions involved but it does suggest that controlled grazing is essential if net lamina production is to be maximised. Controlled grazing as a means of maximising farm production is not new (Smith, 1956) but the concepts of tissue or energy flow upon which this analysis is based are more recent (Hutchinson, 1971).

Hutchinson (1971) advocated the use of energy budgets for defining grazing systems but this approach is probably limited in its application because lamina and not total tissue flow has been demonstrated to be the important flow in grazing systems. Recognition of the importance of lamina rather than total tissue flow in grazing systems may enable more efficient systems of management, which exploit the patterns of lamina rather than total herbage flow, to be evolved. In such systems, lamina flow could possibly be used to control management decisions.

5.7.3 CONCLUSIONS

1. The patterns of tissue flow obtained from this simulation exercise appeared reasonable in the light of the limited corroborative information available.

2. Stocking rates under steady state conditions based on either net herbage or net lamina production were quite different for a large period of the grazing season.

3. Lamina mass is likely to be a better index upon which to base management decisions than either herbage mass or green herbage mass.

4. Tissue flow analysis provides a means by which different grazing managements can be evaluated.

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A P P E N D I X 1

FORTRAN IV ROUTINES FOR HANDLING INDIVIDUAL TILLER OR STOLON DATA

A total of seven routines of varying length and complexity were written to transform raw field length data into forms suitable for statistical analysis. All programs were written in such a manner that both grasses and clovers could be handled by the same program. Source listings for these routines can be obtained from the author.

ROUTINE 'G8 SETUP'

DESCRIPTION

This program transforms raw field data into a standard form. The first two rows contain data describing a primary tiller or stolon and the third row contains data describing daughter tillers or axillary stolons, if present.

CHANNELS

Channel 10 = Input file = raw field data

Channel 11 = Output file = standard form (STD)

RUNNING INSTRUCTIONS

1. Define input and output channels.

2. Requires one 3 digit number (maximum plant unit number e.g. 140, 240, 340 etc) and one 2 digit number (number of sample measurement e.g. 05).

Example: For 60 Poa annua tillers and 5 consecutive measurements = 26005.

ERROR CONDITIONS

The program will upon encountering records out of sequence stop and print out 'RECORDS OUT OF SEQUENCE' 'ERROR'. However, some error conditions remain undetected until other programs are used. These errors

TABLE 1 STATUS CODINGS FOR 'DIFF' FILES

1. Individual Leaves

Status Code	Previous condition	Current condition
510-519	Entire	Decay
520-529	Defoliated	Decay
610-619	Entire	Growth
620-629	Defoliated	Growth
810-819	Entire	Zero growth or decay
820-829	Defoliated	Zero growth or decay
710-719	Entire	Defoliation - tissue lost
720-729	Defoliated	Defoliation - tissue lost
730-739	Entire	Defoliation - zero tissue lost
740-749	Defoliated	Defoliation - zero tissue lost
750-759	Entire	Defoliation - tissue gained
760-769	Defoliated	Defoliation - tissue gained

2. Total Laminae

Status Code	Current condition
630	Decay
640	Zero growth or decay
650	Growth
770	Defoliation - tissue lost
780	Defoliation - zero tissue lost
790	Defoliation - tissue gained

are usually associated with repeats of the same record occurring sequentially, 0 in the number of daughters column - column 16, or errors in the punching of plant number. If an error is made in the definition of 'maximum plant unit number', the routine has no means of detecting the end of the input file and will continue cycling until it incurs a system fault barrier. Particular care therefore is required in defining this parameter.

ROUTINE 'G8 MAIN'

DESCRIPTION

This program is comprised of two major and two minor subroutines. It runs sequentially through the two major subroutines or individually through either routine as required.

Subroutine 'TOTAL' calculates total lamina length, number of days since 31st December, 1968, using subroutine 'CALDYS' and transfers status codes from one record to another if necessary.

Subroutine 'DIFF' calculates the differences between successive records for individual laminae etc. and also a unique set of status codings which describe not only the current condition i.e. defoliated or non-defoliated, growing or dying etc. but also comments on previous history using previous subroutine 'STAT' (Table 1).

CHANNELS

Channel 11 = Input file = STD form data file

Channel 12 = Output file for 'TOTAL' subroutine

Channel 13 = Output file for 'DIFF' subroutine

RUNNING INSTRUCTIONS

1. Define input and output channels.

2. Requires four 2 digit numbers:

   1 = total number of units e.g. 40

   2 = number of sample measurements taken e.g. 05.

   3 = If require 'TOTAL' routine = 00

   If do not require 'TOTAL' subroutine = -1

   4 = If require 'DIFF' routine = 00

   If do not require 'DIFF' routine = -1

Example 1: For entire program to be used using 'TOTAL' and 'DIFF' routines = 40050000.

Example 2: If only 'DIFF' routine required = 4005-100.

ERROR CONDITIONS

The program upon encountering incorrect record sequences in subroutine 'DIFF' will stop and print 'ERROR. RECORDS OUT OF SEQUENCE

IN SBR DIFF(S)'. Usually this means that there is a wrongly coded record or punching errors affecting plant number etc. in the STD file. If this program runs to completion and the final record has been written to the file, then few problems will be encountered in subsequent analyses.

ROUTINE 'G8 CONVERT'

DESCRIPTION

This routine converts lamina, psuedostem (stolon), reproductive stem lengths into areas (lamina only) and weights. It is comprised of 5 subroutines which have separate functions. Lamina area is first calculated and weight per unit area and weight per unit length values then introduced to enable the calculation of weight. It utilises files created by subroutine 'TOTAL' and creates a replica of this file but with area or weight values as appropriate.

Subroutine 'GRASAREA' converts grass lamina length into areas. It requires mid-rib breadth for the youngest leaf, a mean mid-rib breadth for all other leaves together, and the regression coefficient and constant for the regression equation relating actual lamina area as measured by a planimeter to length x breadth lamina area.

Subroutine 'GRASWGHT' converts lamina area, sheath tube and reproductive stem lengths into weights. It requires weights per

unit area for the youngest lamina and the mean of all other leaves, and weight per unit length for the psuedostem and reproductive stem. Daughter tiller laminae area are converted to weight using the weight per unit length of the youngest leaf. Milligrams x 10^{-1} per unit area and per unit length have been found to be the most practical units for this routine.

Subroutine 'CLOVAREA' converts petiole lengths into lamina area, allowing for the proportion of lamina tissue actually present. The regression utilised is a power law equation, the exponent being read in first followed by the constant. This subroutine would have to be changed if another regression model was found to fit the data better.

Subroutine 'CLOVWGHT' converts lamina areas into lamina weight. A separate weight per unit area for the youngest lamina can be used but practical experience indicates that the mean overall weight per unit area for all lamina gives the most orderly results. Milligrams per unit area have proved to be the most practical units.

Subroutine 'PTWGHT' converts petiole and stolon lengths into weights. The same units as for 'CLOVWGHT' routine have proved to be the most practical.

CHANNELS

Channel 12 = Input file = 'TOTAL' length file

Channel 20 = Output file = 'GRASAREA' routine output

Channel 21 = Output file = 'GRASWGHT' routine output

Channel 20 = Output file = 'CLOVAREA' routine output

Channel 21 = Output file = 'CLOVWGHT' routine output

Channel 22 = Output file = 'PETWGHT' routine output

RUNNING INSTRUCTIONS

1. Define channels as required. If grass, then 2 output channels, 20 and 21 required; if clover then 3 output channels, 20, 21 and 22 required. Routines can be called individually as required if necessary.

2. Routines to be called, maximum of 3 - read in free format with space between values.

100 = GRASAREA
101 = GRASWGHT
102 = CLOVAREA
103 = CLOVWGHT
104 = PETWGHT

Example 1: Grass 100 101 0

Example 2: Clover 102 103 104

3. Data values required by routines. All values are read in free format separated by a space and all must be satisfied even with a zero as they are members of arrays. All routines require number of plant units and number of samples.

Example 1: Routine 'GRASAREA' 40 5 0.82 1.61 0.8297 1.5657

Routine 'GRASWGHT' 40 5 0.4175 0.3294 1.9579 1.625

(mg x 10^{-1})

Example 2: Routine 'CLOVAREA' 40 5 0.9428 4.8729

Routine 'CLOVWGHT' 40 5 0.382 0.0382 (mg)

Routine 'PETWGHT' 40 5 0.0414 0.3466 (mg)

ERROR CONDITIONS

No error trapping processes were written into this sequence of routines and if the program stops, 'FORTRAN' diagnostic statements have to be interpreted. If the routine runs normally it will print out on completion 'PROGRAM COMPLETED - STOP'.

ROUTINE 'CLOVMERGE'

DESCRIPTION

This program combines clover lamina and clover petiole, stolon tissue difference files.

CHANNELS

Channel 13 = Input file = Petiole weight difference file.

Channel 14 = Input file = lamina weight difference file.

Channel 15 = Output file = merged petiole plus lamina difference file.

RUNNING INSTRUCTIONS

1. Define input and output channels.
2. Requires number of plant units in file and number of sample measurements read in free format with a space as separator.

Example: 40 5

ERROR CONDITIONS

No error messages were written into this program and if they occur 'FORTRAN' diagnostics will have to be interpreted.

ROUTINE 'G8 BAL'

DESCRIPTION

This program determines growth, decay and the balance of the two processes, net change, in the main program and tissue removed in a subroutine 'DEFOL'. The values printed out are for the interval (e.g. 3 days) and are not daily growth rates etc.

In routine 'DEFOL' which is operated when the status code indicating defoliation is encountered, the growth or decay rate per day of the leaf in question from the previous interval is used to determine the growth that occurred in the current interval. If there is no previous value then the previous value is set at zero. This growth or decay value is added to the measured loss of tissue resultant from defoliation to give tissue removed and then transferred back into the main routine to provide an estimate of growth decay that would have been measured had the plant unit not been defoliated. This model was preferred to that of adding the mean value of growth or decay on the appropriate lamina for all undefoliated plant units, because it was considered that such a model did not adequately describe differences in plant unit size, stage of growth etc.

CHANNELS

Channel 13 = Input file = difference file

Channel 16 = Output file = balance file

RUNNING INSTRUCTIONS

1. Define input and output channels.

2. Program requires two integer values, number of plant units and number of sample measurements read in as 2 digit values with no separator.

Example: 4005 four 40 units and 5 measurements.

ERROR CONDITIONS

The most common error is that of a zero divide which is almost invariably caused by the date being incorrectly punched in the original raw data. The calculation of daily growth or decay rates invokes the use of a time of measurement difference calculated originally from the date. A second error condition, also normally associated with the incorrect punching of the date, is that of an 'invalid real'. This is caused by the value of the 'real' being too large for writing into the space allowed in the 'TOTAL' and 'DIFF' subroutines.

ROUTINE 'G8 MEAN'

DESCRIPTION

This program sums the growth, decay, net change values for a period, converts them to a daily basis, and then means them on a locus basis. This conversion puts the data into a suitable form for analyses by package programs. A correction factor option to change units to whatever scale is desired is included. Care, however, is necessary to ensure that the output values are compatible with the space allocated them. In practice this means convertine mg x 10^{-1}, to mg and mm^2 to cm^2. The correction factor is a 'divisor'.

CHANNELS

Channel 16 = Input file = Balance file

Channel 17 = Output file = Mean file

RUNNING INSTRUCTIONS

1. Define input and output channels.

2. Program requires number of plant units and correction factor in free format with a space as separator. If no correction is required, then '1' is read in.

Example: 40 10

ERROR CONDITIONS

Errors are normally associated with a zero divide, attributable to incorrect data.

ROUTINE 'G8 CONBAL'

DESCRIPTION

This program means tissue removed, severity etc. on a locus basis for a period and also optionally determines frequency and interval between defoliations in subroutines 'FREQ'. Any defoliation

in the first interval is ignored because of the zero growth term. Only plant units with complete records for a period were used in routine 'FREQ'. The output data form is suitable for package analysis. A correction factor option was included identical in use to that described for routine G8 Mean.

CHANNELS

Channel 16 = Input file = balance file

Channel 17 = Output file = conbal file

Channel 18 = Output file = frequency file

RUNNING INSTRUCTIONS

1. Define input and output channels.

2. Program requires number of plant units and correction factor in free format with a space as separator. If no correction is required then '1' is read in.

3. 0 if frequency required, -1 if not required.

Example: 40 10 -1

ERROR CONDITIONS

Errors are normally associated with the zero divide conditions attributable to incorrect data.

DATA HANDLING SEQUENCES

GRASSES

1. Run routine 'G8 SETUP'.
2. Run routine 'G8 MAIN'.
3. Run routine 'G8 CONVERT'.
4. Run routine 'G8 MAIN' routine 'DIFF' only.
5. Run routine 'G8 BAL'.
6. Run routine 'G8 MEAN'.
7. Run routine 'G8 CONBAL'.

CLOVER

1. Run routine 'G8 SETUP'.
2. Run routine 'G8 MAIN'.
3. Run routine 'G8 CONVERT'.
4. Run routine 'G8 MAIN' routine 'DIFF' only.
5. Run routine 'CLOVMERGE'.
6. Run routine 'G8 BAL'.
7. Run routine 'G8 MEAN'.
8. Run routine 'G8 CONBAL'.

A P P E N D I X 2

Variable positions and descriptions for routine G8 SETUP, G8 MAIN, G8 BAL, G8 MEAN and G8 CONBAL.

'G8 SETUP'

VARIABLE	DESCRIPTION
1	Paddock number
2	Plant unit number
3	Sample number
4	Date - 6 digits
5	Column 16 continuation or daughters
6	Status code i.e. replaced, missing
7	Leaf 1 length
8	Leaf 1 status
9	Leaf 2 length
10	Leaf 2 status
11	Leaf 3 length
12	Leaf 3 status
13	Leaf 4 length
14	Leaf 4 status
15	Leaf 5 length
16	Leaf 5 status
17	Sheath tube length
18	Sheath tube status
19	Reproductive stem length
20	Reproductive stem status

Each sample is in 3 consecutive lines of 20 variables.

Line 1 is the main tiller, terminal stolon data.

Line 2 is the continuation of line 1 if required.

Line 3 is the daughter tiller, axillary stolon data.

'G8 MAIN'

SUBROUTINE 'TOTAL'

VARIABLE	DESCRIPTION
Line 1	
1	Paddock number
2	Plant unit number
3	Sample number
4	Day number
5	Month number
6	Year number
7	Column 16 continuation or daughters
8	Status code i.e. replaced, missing
9	Leaf 1 length
10	Leaf 1 status
11	Leaf 2 length
12	Leaf 2 status
13	Leaf 3 length
14	Leaf 3 status
15	Leaf 4 length
16	Leaf 4 status
17	Leaf 5 length
18	Leaf 5 status
19	Sheath tube length
20	Sheath tube status
21	Reproductive stem length
22	Reproductive stem status

SUBROUTINE 'TOTAL'

VARIABLE	DESCRIPTION
Line 2	
1	Leaf 6 length
2	Leaf 6 status
3	Leaf 7 length
4	Leaf 7 status
5	Leaf 8 length
6	Leaf 8 status
7	Leaf 9 length
8	Leaf 9 status
9	Leaf 10 length
10	Leaf 10 status
11	Daughter leaf 1 length
12	Daughter leaf 1 status
13	Daughter leaf 2 length
14	Daughter leaf 2 status
15	Daughter leaf 3 length
16	Daughter leaf 3 status
17	Daughter leaf 4 length
18	Daughter leaf 4 status
19	Daughter leaf 5 length
20	Daughter leaf 5 status
Line 3	
1	Daughter sheath tube length
2	Daughter sheath tube status
3	Number of daughter tillers
4	Total lamina length main tiller
5	Total lamina length daughter tiller
6	Combined (4 & 5) lamina length
7	Number elapsed days since 31.12.68

SUBROUTINE 'DIFF'

VARIABLE	DESCRIPTION
Line 1	
1	Paddock number
2	Plant unit number
3	Sample number
4	Day number
5	Month number
6	Year number
7	Column 16 continuation or daughter
8	Status i.e. replaced or missing
9	Previous record leaf 1 length
10	Previous record leaf 2 length
11	Previous record leaf 3 length
12	Previous record leaf 4 length
13	Previous record leaf 5 length
14	Previous record sheath tube length
15	Previous record reproductive stem length
16	Previous record leaf 6 length
17	Previous record leaf 7 length
18	Previous record leaf 8 length
19	Previous record leaf 9 length
20	Previous record leaf 10 length
Line 2	
1	Previous record daughter leaf 1 length
2	Previous record daughter leaf 2 length
3	Previous record daughter leaf 3 length
4	Previous record daughter leaf 4 length
5	Previous record daughter leaf 5 length

SUBROUTINE 'DIFF'

VARIABLE	DESCRIPTION
6	Previous record daughter sheath tube length
7	Previous record number of daughter tillers
8	Previous record total lamina length main tiller
9	Previous record total lamina length daughter tiller
10	Previous record combined (8 & 9) lamina length
11	Previous record number of elapsed days
12	Leaf 1 length difference
13	Leaf 1 difference status
14	Leaf 2 length difference
15	Leaf 2 difference status
Line 3	
1	Leaf 3 length difference
2	Leaf 3 difference status
3	Leaf 4 length difference
4	Leaf 4 difference status
5	Leaf 5 length difference
6	Leaf 5 difference status
7	Sheath tube length difference
8	Sheath tube difference status
9	Reproductive stem length difference
10	Reproductive stem difference status
11	Leaf 6 length difference
12	Leaf 6 difference status
13	Leaf 7 length difference
14	Leaf 7 difference status

'G8 MAIN'

SUBROUTINE 'DIFF' (CONTD.)

VARIABLE	DESCRIPTION
Line 4	
1	Leaf 8 length difference
2	Leaf 8 difference status
3	Leaf 9 length difference
4	Leaf 9 difference status
5	Leaf 10 length difference
6	Leaf 10 difference status
7	Daughter leaf 1 length difference
8	Daughter leaf 1 difference status
9	Daughter leaf 2 length difference
10	Daughter leaf 2 difference status
11	Daughter leaf 3 length difference
12	Daughter leaf 3 difference status
13	Daughter leaf 4 length difference
14	Daughter leaf 4 difference status
Line 5	
1	Daughter leaf 5 length difference
2	Daughter leaf 5 difference status
3	Daughter sheath tube length difference
4	Daughter sheath tube difference status
5	Number of daughters difference
6	Blank field = 0
7	Total lamina difference main tiller
8	Total lamina main tiller difference status
9	Total lamina difference daughter tiller
10	Total lamina daughter tiller difference status
11	Combined lamina difference
12	Combined lamina difference status
13	Difference in elapsed days between current and previous record
14	Blank field = 0

'G8 BAL'

VARIABLE	DESCRIPTION
Line 1	
1	Paddock number
2	Plant unit number
3	Sample number
4	Sum of main tiller leaves exhibiting growth
5	Number of main tiller leaves exhibiting growth
6	Sum of main tiller leaves exhibiting zero growth
7	Number of main tiller leaves exhibiting zero growth
8	Sum of main tiller leaves exhibiting decay
9	Number of main tiller leaves exhibiting decay
10	Sum of growth + zero + decay on main tiller
11	Total number of leaves on main tiller
12	Growth, zero change, decay of main tiller sheath tube
13	Growth, zero change, decay of main tiller reproductive stem
14	Sum of daughter tiller leaves exhibiting growth
15	Number of daughter tiller leaves exhibiting growth
16	Sum of daughter tiller leaves exhibiting zero growth
17	Number of daughter tiller leaves exhibiting zero growth
18	Sum of daughter tiller leaves exhibiting decay
19	Number of daughter tiller leaves exhibiting decay
20	Sum of growth + zero + decay on daughter tillers
21	Total number of leaves on daughter tiller

VARIABLE	DESCRIPTION
Line 2	
1	Growth, zero change, decay of daughter tiller sheath tube
2	Blank field = 0
3	Sum of growth + zero + decay for both main and daughter tillers
4	Elapsed days between successive records
5	Tissue removed main tiller
6	% severity of defoliation of main tiller
7	Number of leaves defoliated on main tiller
8	Tissue removed daughter tiller
9	% severity of defoliation daughter tiller
10	Number of leaves defoliated on daughter tiller
11	Total tissue removed (main + daughter)
12	% severity of defoliation for total tissue
13	Total number of leaves defoliated
14	Tissue removed main tiller sheath tube
15	% severity of defoliation of main tiller sheath tube
16	Tissue removed main tiller reproductive stem
17	% severity of defoliation of main tiller reproductive stem
Line 3	
1	Previous record main tiller sheath tube
2	Previous record main tiller reproductive stem
3	Previous record daughter tiller sheath tube
4	Previous record number of daughter tillers
5	Previous record total laminae on main tiller
6	Previous record total laminae on daughter tiller
7	Previous record combined total laminae

VARIABLE	DESCRIPTION
Line 3	
1	Combined number of leaves exhibiting decay
2	Combined sum lamina growth + decay
3	Combined total number of leaves
4	Growth, zero change, decay on main tiller sheath tube
5	Growth, zero change, decay on daughter tiller sheath tube
6	Previous main tiller sheath tube
7	Previous daughter tiller sheath tube
8	Mean number of daughter tillers
9	Previous lamina total for main tiller
10	Previous lamina total for daughter tiller
11	Previous combined lamina total
12	Growth, zero change, decay of main tiller reproductive stem

VARIABLE	DESCRIPTION
Line 1	
1	Paddock number
2	Plant unit number
3	Mean leaf tissue removed main tiller
4	Mean % severity leaf tissue removed main tiller
5	Mean number of leaves defoliated on main tiller
6	Mean leaf tissue removed daughter tiller
7	Mean % severity leaf tissue removed daughter tiller
8	Mean number of leaves defoliated on daughter tiller
9	Mean leaf tissue removed combined main + daughter tiller
10	Mean % severity of defoliation combined leaf tissue removed
11	Mean total number of leaves defoliated
Line 2	
1	Mean sheath tube prior to defoliation on main tiller
2	Mean leaf tissue prior to defoliation on main tiller
3	Mean leaf tissue prior to defoliation on daughter tiller
4	Mean combined leaf tissue prior to defoliation
5	Mean amount combined leaf + sheath tissue prior to defoliation
6	Mean sheath tube tissue removed from main tiller
7	Mean % severity sheath tube tissue removed from main tiller

ROUTINE 'FREQ'

VARIABLE	DESCRIPTION
1	Paddock number
2	Plant unit number
3	Number of defoliations in period for main tiller
4	Mean interval (days) between defoliations for main tiller
5	Number of defoliations in period for daughter tiller
6	Mean interval (days) between defoliations for daughter tiller
7	Number of defoliations in period on unit bases
8	Mean interval (days) between defoliations for unit

APPENDIX 3

Table 1. Total and species population densities (units m^{-2}).

Period	Treatment	Ryegrass	Poa annua	White clover	Total
1	500	15 283 d[1/]	11 650 bcd	1 650 a	31 700 cd
	700	20 400 bcd	27 450 a	1 000 a	49 467 ab
	1000	25 550 b	6 800 cd	1 083 a	40 067 bc
	1700	24 483 bc	5 933 d	817 a	31 233 d
2	500	13 267 d	12 167 bcd	1 183 a	26 917 d
	700	37 400 a	15 450 b	1 033 a	53 950 a
	1000	23 833 bc	14 767 bc	400 a	46 000 b
	1700	17 350 cd	11 933 bcd	1 300 a	32 833 cd
	SE	2 642	2 687	573	2 746

Table 2. Number of daughter tillers (stolons) per primary tiller (or stolon).

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	0.45 ab[1/]	0.62 ab	1.87 ab
	700	0.26 ab	0.35 bc	1.86 ab
	1000	0.40 ab	0.55 ab	1.40 c
	1700	0.04 b	0.07 c	0.64 d
2	500	0.53 a	0.83 a	2.27 a
	700	0.13 ab	0.45 abc	1.98 ab
	1000	0.27 ab	0.27 bc	1.82 bc
	1700	0.09 b	0.27 bc	1.63 bc
		SE = 0.15	LSD = 0.43	

1/ Values in columns without common lower case letters are significantly ($P<0.05$) different.

Table 3. Net production on primary tillers and stolons in µg OM tiller (stolon)$^{-1}$ day^{-1}.

Period	Treatment	Ryegrass	Poa annua	White clover
1	500	85 c[1/]	2 c	315 c
	700	92 c	28 bc	286 c
	1000	243 ab	195 a	605 a
	1700	203 b	36 bc	686 a
2	500	60 c	63 bc	234 c
	700	91 c	58 bc	262 c
	1000	320 a	133 ab	302 c
	1700	256 ab	109 abc	484 b
		SE = 38.5	LSD = 110.1	

Table 4. Regression equations of sward height (Y) and leaf area index (Y_1) on herbage mass (HM).

1. Sward height and herbage mass

$$Y = 0.00069\ (\pm 0.00093)\ HM + 1.528652 \times 10^{-6}\ (\pm 4.0942 \times 10^{-7})\ HM^2 + 0.60\ (\pm 0.45).\quad R^2 = 0.93^{***},\quad n = 32.$$

2. Leaf area index and herbage mass

$$Y_1 = 0.00246\ (\pm 0.00034)\ HM - 0.178\ (\pm 0.37)$$

$$R^2 = 0.90^{***},\quad n = 8.$$

Table 5. Regressions of lamina (petiole) tip height, lamina length, ligule height and pseudostem length on herbage mass.

RYEGRASS

Lamina Tip Height

Lamina 1. $Y = 0.024\ (\pm 0.004)\ HM + 1.69\ (\pm 3.90)$, $R^2 = 0.88^{***}$, $n = 8$.
Lamina 2. $Y = 0.032\ (\pm 0.005)\ HM - 6.50\ (\pm 5.81)$, $R^2 = 0.86^{***}$, $n = 8$.
Lamina 3. $Y = 0.021\ (\pm 0.002)\ HM - 4.38\ (\pm 2.29)$, $R^2 = 0.94^{***}$, $n = 8$.

Lamina Length

Lamina 1. $Y = 0.014\ (\pm 0.002)\ HM + 5.57\ (\pm 2.46)$, $R^2 = 0.86^{***}$, $n = 8$.
Lamina 2. $Y = 0.011\ (\pm 0.006)\ HM + 10.71\ (\pm 6.06)$, $R^2 = 0.43^{P=0.08}$, $n = 8$.
Lamina 3. $Y = 0.009\ (\pm 0.004)\ HM + 3.81\ (\pm 4.66)$, $R^2 = 0.44^{P=0.07}$, $n = 8$.

Ligule[1] Height. $Y = 0.015(\pm 0.001)HM - 2.96\ (\pm 1.21)$, $R^2 = 0.97^{***}$, $n = 8$.

Pseudostem Length. $Y = 0.015\ (\pm 0.001)HM + 0.41\ (\pm 0.60)$, $R^2 = 0.99^{***}$, $n = 8$.

POA ANNUA

Lamina Tip Height

Lamina 1. $Y = 0.019\ (\pm 0.002)\ HM - 2.24\ (\pm 2.57)$, $R^2 = 0.92^{***}$, $n = 8$.
Lamina 2. $Y = 0.019\ (\pm 0.001)\ HM - 0.45\ (\pm 1.33)$, $R^2 = 0.98^{***}$, $n = 8$.
Lamina 3. $Y = 0.018\ (\pm 0.001)\ HM - 4.01\ (\pm 1.44)$, $R^2 = 0.97^{***}$, $n = 8$.

continued ...

Table 5 continued

Lamina Length

Lamina 1. $Y = 0.008\ (\pm 0.002)\ HM + 1.78\ (\pm 2.24)$, $R^2 = 0.74^{**}$, n = 8.

Lamina 2. $Y = 0.011\ (\pm 0.001)\ HM + 4.05\ (\pm 1.18)$, $R^2 = 0.95^{***}$, n = 8.

Lamina 3. $Y = 0.011\ (\pm 0.001)\ HM + 3.52\ (\pm 0.98)$, $R^2 = 0.96^{***}$, n = 8.

Ligule[1] Height. $Y = 0.013\ (\pm 0.001)\ HM - 2.52\ (\pm 1.24)$, $R^2 = 0.96^{***}$, n = 8.

Pseudostem Length. $Y = 0.011\ (\pm 0.002)\ HM + 3.87\ (\pm 1.65)$, $R^2 = 0.91^{***}$, n = 8.

CLOVER

Petiole Tip Height

Petiole 1. $Y = 0.004\ (\pm 0.001)\ HM + 2.26\ (\pm 1.45)$, $R^2 = 0.66^{**}$, n = 8.

Petiole 2. $Y = 0.024\ (\pm 0.002)\ HM - 6.27\ (\pm 1.88)$, $R^2 = 0.97^{***}$, n = 8.

Petiole 3. $Y = 0.023\ (\pm 0.002)\ HM - 7.54\ (\pm 2.42)$, $R^2 = 0.95^{***}$, n = 8.

1) Ligule height is the vertical distance from the ligule of the penultimate youngest leaf to the soil surface.

Table 6. Regression models of total organic matter intake (OM_T) versus herbage mass (HM).

Logistic model

Ewe:

$$OM_T = \frac{2724\ (\pm 714)}{1 + 9.22\ (\pm 5.55)\ e} - 0.00231\ (\pm 0.0012)\ HM$$

$R^2 = 0.89^{**}$, RMS = 7.7552×10^4, n = 8.

Lamb:

$$OM_T = \frac{944\ (\pm 90)}{1 + 24.9\ (\pm 23.8)\ e} - 0.00435\ (\pm 0.00138)\ HM$$

$R^2 = 0.88^{**}$, RMS = 1.4436×10^4, n = 8.

Ewe + Lamb:

$$OM_T = \frac{3483\ (\pm 351)}{1 + 11.8\ (\pm 6.3)\ e} - 0.00295\ (\pm 0.00084)\ HM$$

$R^2 = 0.94^{***}$, RMS = 7.1533×10^4, n = 8.

Linear model

Ewe:

$OM_T = 1.31\ (\pm 0.19)\ HM + 66.8\ (\pm 209)$

$R^2 = 0.89^{***}$, RMS = 6.5004×10^4, n = 8.

Lamb:

$OM_T = 0.50\ (\pm 0.12)\ HM + 96\ (\pm 130)$

$R^2 = 0.75^{**}$, RMS = 2.5072×10^4, n = 8.

Ewe + Lamb:

$OM_T = 1.81\ (\pm 0.23)\ HM + 160\ (\pm 250)$

$R^2 = 0.91^{***}$, RMS = 9.2913×10^4, n = 8.

Table 7. Regressions of green organic matter intake (OM_G) versus herbage mass (HM).

Logistic model

Ewe:

$$OM_G = \frac{2528\ (\pm 673)}{1 + 11.2\ (\pm 9.48)\ e} - 0.00259\ (\pm 0.00155)\ HM$$

$R^2 = 0.87^{**}$, RMS = 9.2349×10^4, n = 8.

Lamb:

$$OM_G = \frac{886\ (\pm 68)}{1 + 34.9\ (\pm 30.6)\ e} - 0.0048\ (\pm 0.00125)\ HM$$

$R^2 = 0.92^{**}$, RMS = 8.809×10^3, n = 8.

Ewe + Lamb:

$$OM_G = \frac{3251\ (\pm 328)}{1 + 15.9\ (\pm 11.2)\ e} - 0.00336\ (\pm 0.00106)\ HM$$

$R^2 = 0.93^{***}$, RMS = 8.9954×10^4, n = 8.

Linear model

Ewe:

$OM_G = 1.31\ (\pm 0.21)\ HM - 4.5\ (\pm 228)$

$R^2 = 0.87^{***}$, RMS = 7.7261×10^4, n = 8.

Lamb:

$OM_G = 0.48\ (\pm 0.11)\ HM + 72.7\ (\pm 119.2)$

$R^2 = 0.77^{**}$, RMS = 2.1134×10^4, n = 8.

Ewe + Lamb:

$OM_G = 1.79\ (\pm 0.24)\ HM - 68.3\ (\pm 269.3)$

$R^2 = 0.90^{***}$, RMS = 1.0794×10^5, n = 8.

Table 8. Regressions of lamina organic matter intake (OM_L) versus herbage mass (HM).

Logistic model

Ewe:

$$OM_L = \frac{2020\ (\pm 333)}{1 + 22.7\ (\pm 29.2)\ e} - 0.00366\ (\pm 0.0019)\ HM$$

$R^2 = 0.85^{**}$, HMS = 9.4859×10^4, n = 8.

Lamb:

$$OM_L = \frac{770\ (\pm 44)}{1 + 77.3\ (\pm 63.9)\ e} - 0.00583\ (\pm 0.00117)\ HM$$

$R^2 = 0.96^{***}$, RMS = 4.209×10^3, n = 8.

Ewe + Lamb:

$$OM_L = \frac{2745\ (\pm 254)}{1 + 31.1\ (\pm 28.6)\ e} - 0.00428\ (\pm 0.00132)\ HM$$

$R^2 = 0.92^{**}$, RMS = 8.9149×10^4, n = 8.

Linear model

Ewe:

$OM_L = 1.20\ (\pm 0.22)\ HM - 81\ (\pm 238)$

$R^2 = 0.84^{**}$, RMS = 8.4205×10^4, n = 8.

Lamb:

$OM_L = 0.45\ (\pm 0.10)\ HM + 32\ (\pm 111)$

$R^2 = 0.76^{**}$, RMS = 1.8631×10^4, n = 8.

Ewe + Lamb:

$OM_L = 1.65\ (\pm 0.26)\ HM - 49\ (\pm 288)$

$R^2 = 0.87^{***}$, RMS = 1.2334×10^5, n = 8.

Table 9 Ewe and lamb liveweight change from prior to period 1 to after period 2 (g LWG animal^{-1} day^{-1}).

Treatment	Ewes	Lambs
500	- 144 b[1/]	61 b
700	- 56 b	117 b
1000	93 a	267 a
1700	113 a	340 a
SE	34.4	22.9

1/ Values in columns without common lower case letters are significantly ($P < 0.05$) different.

Table 10 Comparison of senescence rates directly and indirectly measured (kg DM (OM) ha^{-1} day^{-1}).

A. S_M values taken from table 3.3.5.10

Period	Treatment	G_L	C_L	(G_L - C_L = S_L)	S_M
1	500	25.9	15.2[1/]	10.7	9.2
	700	57.6	38.2	19.4	40.9
	1000	80.7	36.7	44.0	23.7
	1700	80.7	38.1	42.6	47.3
2	500	22.8	17.2[2/]	5.6	10.5
	700	53.2	28.8	24.2	23.5
	1000	51.1	25.1	26.0	25.8
	1700	55.1	31.3	23.8	34.7

continued ...

Table 10 continued

B. S_M values derived from equation 3.3.5.5.

Period	Treatment	G_L 3/	C_L	($G_L - C_L = S_L$)	S_M
1	500	25.6	15.2 1/	10.4	12.6
	700	57.8	38.2	19.6	16.6
	1000	79.8	36.7	43.1	23.9
	1700	81.4	38.1	43.3	42.5
2	500	26.2	17.2 2/	9.0	11.4
	700	44.4	28.8	15.6	16.3
	1000	53.7	25.1	28.6	24.4
	1700	58.0	31.3	26.7	38.5

1/ 18.3 kg DM ha^{-1} day^{-1} deducted from total lamina consumption.

2/ 17.7 kg DM ha^{-1} day^{-1} deducted from total lamina consumption.

3/ G_L values derived from period equations in table 3.3.5.14.

Table 11 Mean and standard error [1/] of mean of interval between successive defoliations (days).

Period	Treatment	Ryegrass			Poa annua			White clover		
		Mean	SE	n	Mean	SE	n	Mean	SE	n
1	500	5.57	0.50	98	6.42	0.42	131	5.31	0.24	102
	700	4.10	0.56	76	8.93	0.28	126	5.00	0.39	64
	1000	8.31	0.35	113	13.80	3.06	127	6.28	0.49	98
	1700	10.54	2.83	118	14.48	2.98	139	7.87	0.40	107
2	500	5.38	0.49	103	7.61	0.40	116	5.53	0.50	98
	700	8.75	0.32	107	10.60	2.86	116	5.45	0.55	81
	1000	10.60	3.03	103	15.90	3.46	112	5.81	0.58	73
	1700	17.50	3.52	117	15.37	3.59	101	8.85	0.33	91

1/ After Fenlon (1978) and personal communication.

Table 12 Mean and standard error of mean of tissue removed by grazing per locus per defoliation (mg).

Period	Treatment	Ryegrass			Poa annua			White clover		
		Mean	SE	n	Mean	SE	n	Mean	SE	n
1	500	0.70	0.01	28	0.05	0.01	21	2.47	0.42	30
	700	0.74	0.11	38	0.61	0.08	19	2.32	0.46	37
	1000	2.41	0.38	29	0.75	0.19	18	3.05	0.45	26
	1700	1.75	0.37	18	0.25	0.04	20	4.41	0.64	30
2	500	0.64	0.13	33	0.60	0.11	23	2.38	0.40	32
	700	0.75	0.09	30	0.45	0.13	21	2.21	0.32	38
	1000	1.40	0.20	21	1.17	0.20	18	2.33	0.32	37
	1700	1.91	0.41	18	0.97	0.19	19	3.60	0.67	33

A P P E N D I X 4

ANALYSIS OF VARIANCE TABLES FOR EXPERIMENT 1

1. The population density data was analysed over three periods, May, period 1 and and Period 2 and therefore the degrees of freedom for time are 2.

2. Data for primary units in ANOVA tables are in mg.

3. Where tabular data has not been given in the main text, it is given at the foot of the appropriate ANOVA table.

ANALYSIS OF VARIANCE

VARIATE: RYEGRASS POPULATION DENSITY

SOURCE OF VARIATION	DF		SS	SS%		MS	VR
SAMPLE STRATUM	11	2.446E	9	12.31	2.223E	8	2.653
SAMPLE. UNITS STRATUM							
PADDOCKS	3	1.849E	9	9.30	6.163E	8	7.353
TIME	2	2.485E	9	12.51	1.243E	9	14.828
PADDOCKS. TIME	6	2.949E	9	14.84	4.916E	8	5.865
RESIDUAL	121	1.014E	10	51.04	8.381E	7	
TOTAL	132	1.742E	10	87.69	1.320E	8	
GRAND TOTAL	143	1.987E	10	100.00			
GRAND MEAN	19292						
TOTAL NUMBER OF OBSERVATIONS	144						

ANALYSIS OF VARIANCE

VARIATE: POA ANNUA POPULATION DENSITY

SOURCE OF VARIATION	DF		SS	SS%		MS	VR
SAMPLE STRATUM	11	1.461E	9	9.29	1.328E	8	1.533
SAMPLE. UNITS STRATUM							
PADDOCKS	3	1.500E	9	9.54	5.000E	8	5.773
TIME	2	7.946E	7	0.51	3.973E	7	0.459
PADDOCKS. TIME	6	2.203E	9	14.01	3.672E	8	4.239
RESIDUAL	121	1.048E	10	66.65	8.662E	7	
TOTAL	132	1.426E	10	90.71	1.081E	8	
GRAND TOTAL	143	1.572E	10	100.00			
GRAND MEAN		13763					
TOTAL NUMBER OF OBSERVATIONS		144					

ANALYSIS OF VARIANCE

VARIATE: WHITE CLOVER POPULATION DENSITY

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
SAMPLE STRATUM	11	37359984	7.10	3396362	0.862
SAMPLE. UNITS STRATUM					
PADDOCKS	3	3686665	0.70	1228888	0.312
TIME	2	1581665	0.30	790833	0.201
PADDOCKS. TIME	6	6758328	1.28	1126388	0.286
RESIDUAL	121	476612608	90.61	3938947	
TOTAL	132	488639232	92.90	3701812	
GRAND TOTAL	143	525999104	100.00		
GRAND MEAN		1000			
TOTAL NUMBER OF OBSERVATIONS		144			

ANALYSIS OF VARIANCE

VARIATE: TOTAL POPULATION DENSITY

SOURCE OF VARIATION	DF		SS	SS%		MS	VR
SAMPLE STRATUM	11	1.565E	9	6.81	1.423E	8	1.573
SAMPLE. UNITS STRATUM							
PADDOCKS	3	5.124E	9	22.28	1.708E	9	18.884
TIME	2	2.393E	9	10.41	1.196E	9	13.228
PADDOCKS. TIME	6	2.968E	9	12.91	4.946E	8	5.469
RESIDUAL	121	1.094E	10	47.59	9.044E	7	
TOTAL	132	2.143E	10	93.19	1.623E	8	
GRAND TOTAL	143	2.299E	10	100.00			
GRAND MEAN		36186					
TOTAL NUMBER OF OBSERVATIONS		144					

ANALYSIS OF VARIANCE

VARIATE: NUMBER OF DAUGHTERS PER PRIMARY UNIT

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		1.6661	0.12	1.6661	1.841
TRANSECT. TILLERS STRATUM	8		4.7077	0.35	0.5885	0.650
TRANSECT. TILLERS. UNITS STRATUM						
TIME	1		6.8149	0.50	6.8149	7.531
SPECIES	2		384.8950	28.25	192.4475	212.659
PADDOCKS	3		49.1884	3.61	16.3961	18.118
QUARTERS	3		2.2150	0.16	0.7383	0.816
TIME. SPECIES	2		12.1249	0.89	6.0625	6.699
TIME. PADDOCKS	3		6.6866	0.49	2.2289	2.463
SPECIES. PADDOCKS	6		11.9224	0.88	1.9871	2.196
TIME. QUARTERS	3		4.7013	0.35	1.5671	1.732
SPECIES. QUARTERS	6		8.6709	0.64	1.4451	1.597
PADDOCKS. QUARTERS	9		16.2387	1.19	1.8043	1.994
TIME. SPECIES. PADDOCKS	6		5.3545	0.39	0.8924	0.986
TIME. SPECIES. QUARTERS	6		4.1105	0.30	0.6851	0.757
TIME. PADDOCKS. QUARTERS	9		13.8212	1.01	1.5357	1.697
SPECIES. PADDOCKS. QUARTERS	18		43.7161	3.21	2.4287	2.684
RESIDUAL	869	(4)	786.4087	57.72	0.9050	
TOTAL	946		1356.8674	99.58	1.4343	
GRAND TOTAL	955		1363.2410	100.05		

ESTIMATED GRAND MEAN 0.793
TOTAL NUMBER OF OBSERVATIONS 960
NUMBER OF MISSING VALUES 4

ANALYSIS OF VARIANCE

VARIATE: LEAF AREA PER PRIMARY UNIT

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.2490	0.07	0.2490	1.075
TRANSECT. TILLER STRATUM	8	2.7148	0.72	0.3393	1.466
TRANSECT. TILLER. UNITS STRATUM					
MONTH	1	4.7461	1.26	4.7461	20.499
SPECIES	2	1.2842	0.34	0.6421	2.773
PADDOCK	3	132.9481	35.20	44.3160	191.411
QUARTER	3	2.5469	0.67	0.8490	3.667
MONTH. SPECIES	2	0.4572	0.12	0.2286	0.987
MONTH. PADDOCK	3	4.6297	1.23	1.5432	6.666
SPECIES. PADDOCK	6	1.8901	0.50	0.3150	1.361
MONTH. QUARTER	3	0.9891	0.26	0.3297	1.424
SPECIES. QUARTER	6	0.8104	0.21	0.1351	0.583
PADDOCK. QUARTER	9	5.4942	1.45	0.6105	2.637
MONTH. SPECIES. PADDOCK	6	0.6328	0.17	0.1055	0.456
MONTH. SPECIES. QUARTER	6	1.4775	0.39	0.2463	1.064
MONTH. PADDOCK. QUARTER	9	2.2727	0.60	0.2525	1.091
SPECIES. PADDOCK. QUARTER	18	12.3764	3.28	0.6876	2.970
RESIDUAL	873	202.1198	53.52	0.2315	
TOTAL	950	374.6748	99.21	0.3944	
GRAND TOTAL	959	377.6384	100.00		

GRAND MEAN 0.726
TOTAL NUMBER OF OBSERVATIONS 960

ANALYSIS OF VARIANCE

VARIATE: LEAF AREA INDEX

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.2900	0.03	0.2900	0.777
TRANSECT. TILLER STRATUM	8	3.2873	0.30	0.4109	1.100
TRANSECT. TILLER. UNITS STRATUM					
MONTH	1	6.7885	0.61	6.7885	18.176
SPECIES	2	355.3379	32.07	177.6689	475.705
PADDOCK	3	138.8340	12.53	46.2780	123.908
QUARTER	3	4.0082	0.36	1.3361	3.577
MONTH. SPECIES	2	12.5766	1.13	6.2883	16.837
MONTH. PADDOCK	3	15.6828	1.42	5.2276	13.997
SPECIES. PADDOCK	6	156.0459	14.08	26.0076	69.635
MONTH. QUARTER	3	1.7172	0.15	0.5724	1.533
SPECIES. QUARTER	6	2.0371	0.18	0.3395	0.909
PADDOCK QUARTER	9	3.9282	0.35	0.4365	1.169
MONTH. SPECIES. PADDOCK	6	64.4037	5.81	10.7340	28.740
MONTH. SPECIES. QUARTER	6	1.1190	0.10	0.1865	0.499
MONTH. PADDOCK. QUARTER	9	3.2647	0.29	0.3627	0.971
SPECIES. PADDOCK. QUARTER	18	12.6972	1.15	0.7054	1.889
RESIDUAL	873	326.0530	29.43	0.3735	
TOTAL	950	1104.4922	99.68	1.1626	
GRAND TOTAL	959	1108.0693	100.00		

GRAND MEAN 0.754
TOTAL NUMBER OF OBSERVATIONS 960

ANALYSIS OF VARIANCE

VARIATE: LAMINA GROWTH PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.00011	0.00	0.00011	0.005
TRANSECT. TILLERS STRATUM	8	0.15305	0.35	0.01913	0.842
TRANSECT. TILLERS. UNITS STRATUM					
TIME	1	0.76297	1.72	0.76297	33.584
SPECIES	2	13.55364	30.64	6.77682	298.303
PADDOCKS	3	3.50592	7.93	1.16864	51.441
QUARTERS	3	0.19823	0.45	0.06608	2.909
TIME. SPECIES	2	0.91939	2.08	0.45970	20.235
TIME. PADDOCKS	3	0.51269	1.16	0.17090	7.523
SPECIES. PADDOCKS	6	2.39948	5.42	0.39991	17.603
TIME. QUARTERS	3	0.06521	0.15	0.02174	0.957
SPECIES. QUARTERS	6	0.20166	0.46	0.03361	1.479
PADDOCKS. QUARTERS	9	0.45891	1.04	0.05099	2.244
TIME. SPECIES. PADDOCKS	6	0.51922	1.17	0.08654	3.809
TIME. SPECIES. QUARTERS	6	0.16242	0.37	0.02707	1.192
TIME. PADDOCKS. QUARTERS	9	0.12847	0.29	0.01427	0.628
SPECIES. PADDOCKS. QUARTERS	18	0.99580	2.25	0.05532	2.435
RESIDUAL	869 (4)	19.74185	44.63	0.02272	
TOTAL	946	44.12578	99.76	0.04664	
GRAND TOTAL	955	44.27893	100.10		

ESTIMATED GRAND MEAN	0.2036
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: PSEUDOSTEM (STOLON) GROWTH PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.02221	0.09	0.02221	1.095
TRANSECT. TILLERS STRATUM	8	0.20851	0.87	0.02606	1.285
TRANSECT. TILLERS. UNITS STRATUM					
TIME	1	0.00462	0.02	0.00462	0.228
SPECIES	2	0.33615	1.41	0.16808	8.285
PADDOCKS	3	1.52474	6.39	0.50825	25.053
QUARTERS	3	0.63691	2.67	0.21230	10.465
TIME. SPECIES	2	0.54269	2.27	0.27134	13.375
TIME. PADDOCKS	3	0.05474	0.23	0.01825	0.899
SPECIES. PADDOCKS	6	0.42163	1.77	0.07027	3.464
TIME. QUARTERS	3	0.10063	0.42	0.03354	1.653
SPECIES. QUARTERS	6	0.09889	0.41	0.01648	0.812
PADDOCKS. QUARTERS	9	0.37274	1.56	0.04142	2.041
TIME. SPECIES. PADDOCKS	6	0.72380	3.03	0.12063	5.946
TIME. SPECIES. QUARTERS	6	0.27155	1.14	0.04526	2.341
TIME. PADDOCKS. QUARTERS	9	0.29951	1.26	0.03328	1.640
SPECIES. PADDOCKS. QUARTERS	18	0.62024	2.60	0.03446	1.698
RESIDUAL	869 (4)	17.62956	73.88	0.02029	
TOTAL	946	23.63840	99.06	0.02499	
GRAND TOTAL	955	23.86911	100.03		

ESTIMATED GRAND MEAN	0.0707
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: TOTAL GROWTH PER PRIMARY UNIT

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		0.05334	0.06	0.05334	1.006
TRANSECT. TILLERS STRATUM	8		0.44248	0.50	0.05531	1.043
TRANSECT. TILLERS. UNITS STRATUM						
TIME	1		0.50504	0.57	0.50504	9.526
SPECIES	2		14.14962	16.10	7.07481	133.444
PADDOCKS	3		11.27992	12.83	3.75997	70.920
QUARTERS	3		1.80966	2.06	0.60322	11.378
TIME. SPECIES	2		2.18030	2.48	1.09015	20.562
TIME. PADDOCKS	3		0.36700	0.42	0.12233	2.307
SPECIES. PADDOCKS	6		3.74689	4.26	0.62448	11.779
TIME. QUARTERS	3		0.18551	0.21	0.06184	1.166
SPECIES. QUARTERS	6		0.19848	0.23	0.03308	0.624
PADDOCKS. QUARTERS	9		1.31680	1.50	0.14631	2.760
TIME. SPECIES. PADDOCKS	6		2.32682	2.65	0.38780	7.315
TIME. SPECIES. QUARTERS	6		0.85367	0.97	0.14228	2.684
TIME. PADDOCKS. QUARTERS	9		0.78719	0.90	0.08747	1.650
SPECIES. PADDOCKS. QUARTERS	18		1.68622	1.92	0.09368	1.767
RESIDUAL	869	(4)	46.07187	52.42	0.05302	
TOTAL	946		87.46492	99.51	0.09246	
GRAND TOTAL	955		87.96074	100.07		

ESTIMATED GRAND MEAN	0.2915
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: LAMINA SENESCENCE PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.02239	0.15	0.02239	1.751
TRANSECT. TILLERS STRATUM	8	0.19362	1.30	0.02420	1.893
TRANSECT. TILLERS. UNITS STRATUM					
TIME	1	0.03483	0.23	0.03483	2.724
SPECIES	2	0.19062	1.28	0.09531	7.454
PADDOCKS	3	1.00696	6.77	0.33565	26.252
QUARTERS	3	0.24154	1.62	0.08051	6.297
TIME. SPECIES	2	0.14592	0.98	0.07296	5.706
TIME. PADDOCKS	3	0.08109	0.55	0.02703	2.114
SPECIES. PADDOCKS	6	0.32443	2.18	0.05407	4.229
TIME. QUARTERS	3	0.08888	0.60	0.02963	2.317
SPECIES. QUARTERS	6	0.05556	0.37	0.00926	0.724
PADDOCKS. QUARTERS	9	0.15739	1.06	0.01749	1.368
TIME. SPECIES. PADDOCKS	6	0.59379	3.99	0.09897	7.740
TIME. SPECIES. QUARTERS	6	0.20088	1.35	0.03348	2.619
TIME. PADDOCKS. QUARTERS	9	0.14996	1.01	0.01666	1.303
SPECIES. PADDOCKS. QUARTERS	18	0.27655	1.86	0.01536	1.202
RESIDUAL	869 (4)	11.11094	74.73	0.01279	
TOTAL	946	14.65933	98.59	0.01550	
GRAND TOTAL	955	14.87534	100.05		

ESTIMATED GRAND MEAN	-0.0772
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: NET PRODUCTION PER PRIMARY UNIT

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		0.02571	0.05	0.02571	0.782
TRANSECT. TILLERS STRATUM	8		0.25752	0.50	0.03219	0.979
TRANSECT. TILLERS. UNITS STRATUM						
TIME	1		0.47176	0.91	0.47176	14.347
SPECIES	2		16.53423	32.04	8.26711	251.416
PADDOCKS	3		1.09663	2.13	0.36554	11.117
QUARTERS	3		0.39324	0.76	0.13108	3.986
TIME. SPECIES	2		0.39130	0.76	0.19565	5.950
TIME. PADDOCKS	3		0.42476	0.82	0.14159	4.306
SPECIES. PADDOCKS	6		1.42145	2.75	0.23691	7.205
TIME. QUARTERS	3		0.12180	0.24	0.04060	1.235
SPECIES. QUARTERS	6		0.19067	0.37	0.03178	0.966
PADDOCKS. QUARTERS	9		0.26121	0.51	0.02902	0.883
TIME. SPECIES. PADDOCKS	6		0.21510	0.42	0.03585	1.090
TIME. SPECIES. QUARTERS	6		0.36393	0.71	0.06066	1.845
TIME. PADDOCKS. QUARTERS	9		0.16538	0.32	0.01838	0.559
SPECIES. PADDOCKS. QUARTERS	18		0.75623	1.47	0.04201	1.278
RESIDUAL	869	(4)	28.57469	55.37	0.03288	
TOTAL	946		51.38231	99.57	0.05432	
GRAND TOTAL	955		51.66553	100.12		

ESTIMATED GRAND MEAN	0.1264
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: LAMINA GROWTH PER UNIT AREA

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		4.3	0.00	4.3	0.014
TRANSECT. TILLERS STRATUM	8		3362.5	0.51	420.3	1.348
TRANSECT. TILLERS. UNITS STRATUM						
TIME	1		6576.0	0.99	6576.0	21.088
SPECIES	2		224384.0	33.75	112192.0	359.771
PADDOCKS	3		32343.7	4.87	10781.2	34.573
QUARTERS	3		4149.2	0.62	1383.1	4.435
TIME SPECIES	2		20601.3	3.10	10300.6	33.031
TIME. PADDOCKS	3		3883.4	0.58	1294.5	4.151
SPECIES. PADDOCKS	6		49590.6	7.46	8265.1	26.504
TIME. QUARTERS	3		1221.3	0.18	407.1	1.306
SPECIES. QUARTERS	6		1915.6	0.29	319.3	1.024
PADDOCKS. QUARTERS	9		1303.4	0.20	144.8	0.464
TIME. SPECIES. PADDOCKS	6		36491.7	5.49	6081.9	19.503
TIME. SPECIES. QUARTERS	6		2463.0	0.37	410.5	1.316
TIME. PADDOCKS. QUARTERS	9		1565.5	0.24	173.9	0.558
SPECIES. PADDOCKS. QUARTERS	18		4241.9	0.64	235.7	0.756
RESIDUAL	869	(4)	270991.3	40.76	311.8	
TOTAL	946		661721.4	99.54	699.5	
GRAND TOTAL	955		665088.1	100.05		

ESTIMATED GRAND MEAN	17.80
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: PSEUDOSTEM (STOLON) GROWTH RATE PER UNIT AREA

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		21.3	0.00	21.3	0.064
TRANSECT. TILLERS STRATUM	8		1868.7	0.43	233.6	0.698
TRANSECT. TILLERS. UNITS STRATUM						
TIME	1		3206.1	0.75	3206.1	9.587
SPECIES	2		28388.2	6.60	14194.1	42.444
PADDOCKS	3		16121.2	3.75	5373.7	16.069
QUARTERS	3		5095.2	1.18	1698.4	5.079
TIME. SPECIES	2		3243.2	0.75	1621.6	4.849
TIME. PADDOCKS	3		7614.3	1.77	2538.1	7.590
SPECIES. PADDOCKS	6		21430.6	4.98	3571.8	10.681
TIME. QUARTERS	3		3882.2	0.90	1294.1	3.870
SPECIES. QUARTERS	6		6023.7	1.40	1004.0	3.002
PADDOCKS. QUARTERS	9		3611.1	0.84	401.2	1.200
TIME. SPECIES. PADDOCKS	6		12295.1	2.86	2049.2	6.128
TIME. SPECIES. QUARTERS	6		6606.2	1.54	1101.0	3.292
TIME. PADDOCKS. QUARTERS	9		11959.3	2.78	1328.8	3.973
SPECIES. PADDOCKS. QUARTERS	18		8054.8	1.87	447.5	1.338
RESIDUAL	869	(4)	290610.2	67.58	334.4	
TOTAL	946		428141.1	99.57	452.6	
GRAND TOTAL	955		430031.1	100.01		

ESTIMATED GRAND MEAN	6.10
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: TOTAL GROWTH PER UNIT AREA

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		82.1	0.01	82.1	0.105
TRANSECT. TILLERS STRATUM	8		5492.4	0.36	686.6	0.874
TRANSECT. TILLERS. UNITS STRATUM						
TIME	1		57.0	0.00	57.0	0.073
SPECIES	2		421922.9	27.84	210961.4	268.615
PADDOCKS	3		105478.7	6.96	35159.6	44.768
QUARTERS	3		20591.1	1.36	6863.7	8.740
TIME. SPECIES	2		6859.1	0.45	3429.5	4.367
TIME. PADDOCKS	3		1958.5	0.13	652.8	0.831
SPECIES. PADDOCKS	6		144573.4	9.54	24095.6	30.681
TIME. QUARTERS	3		7784.2	0.51	2594.7	3.304
SPECIES. QUARTERS	6		14891.0	0.98	2481.8	3.160
PADDOCKS. QUARTERS	9		5119.8	0.34	568.9	0.724
TIME. SPECIES. PADDOCKS	6		49259.7	3.25	8209.9	10.454
TIME. SPECIES. QUARTERS	6		20208.1	1.33	3368.0	4.288
TIME. PADDOCKS. QUARTERS	9		18478.2	1.22	2053.1	2.614
SPECIES. PADDOCKS. QUARTERS	18		10531.1	0.69	585.1	0.745
RESIDUAL	869	(4)	682482.9	45.04	785.4	
TOTAL	946		1510195.0	99.66	1596.4	
GRAND TOTAL	955		1515769.0	100.03		

ESTIMATED GRAND MEAN	25.79
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: LAMINA SENESCENCE PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	1231.7	0.33	1231.7	4.305
TRANSECT. TILLERS STRATUM	8	2438.0	0.65	304.8	1.065
TRANSECT. TILLERS. UNITS STRATUM					
TIME	1	1172.9	0.31	1172.9	4.099
SPECIES	2	45567.5	12.19	22783.8	79.627
PADDOCKS	3	13909.1	3.72	4636.4	16.204
QUARTERS	3	2046.6	0.55	682.2	2.384
TIME. SPECIES	2	3351.3	0.90	1675.7	5.856
TIME. PADDOCKS	3	1909.9	0.51	636.6	2.225
SPECIES. PADDOCKS	6	22208.7	5.94	3701.4	12.936
TIME. QUARTERS	3	470.1	0.13	156.7	0.548
SPECIES. QUARTERS	6	1685.8	0.45	281.0	0.982
PADDOCKS. QUARTERS	9	2797.9	0.75	310.9	1.086
TIME. SPECIES. PADDOCKS	6	14846.2	3.97	2474.4	8.648
TIME. SPECIES. QUARTERS	6	2871.4	0.77	478.6	1.673
TIME. PADDOCKS. QUARTERS	9	3399.2	0.91	377.7	1.320
SPECIES. PADDOCKS. QUARTERS	18	5237.4	1.40	291.0	1.017
RESIDUAL	869 (4)	248649.6	66.54	286.1	
TOTAL	946	370123.3	99.05	391.3	
GRAND TOTAL	955	373792.9	100.03		

ESTIMATED GRAND MEAN	-8.97
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: NET PRODUCTION PER UNIT AREA

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		1949.9	0.16	1949.9	2.102
TRANSECT. TILLERS STRATUM	8		5091.3	0.40	636.4	0.686
TRANSECT. TILLERS. UNITS STRATUM						
TIME	1		712.8	0.06	712.8	0.768
SPECIES	2		197673.6	15.72	98836.8	106.540
PADDOCKS	3		59627.5	4.74	19875.8	21.425
QUARTERS	3		18821.8	1.50	6273.9	6.763
TIME. SPECIES	2		2056.1	0.16	1028.1	1.108
TIME. PADDOCKS	3		448.5	0.04	149.5	0.161
SPECIES. PADDOCKS	6		71816.8	5.71	11969.5	12.902
TIME. QUARTERS	3		9413.6	0.75	3137.9	3.382
SPECIES. QUARTERS	6		17368.5	1.38	2894.8	3.120
PADDOCKS. QUARTERS	9		7093.5	0.56	788.2	0.850
TIME. SPECIES. PADDOCKS	6		10944.3	0.87	1824.1	1.966
TIME. SPECIES. QUARTERS	6		19888.2	1.58	3314.7	3.573
TIME. PADDOCKS. QUARTERS	9		13005.9	1.03	1445.1	1.558
SPECIES. PADDOCKS. QUARTERS	18		15624.7	1.24	868.0	0.936
RESIDUAL	869	(4)	806171.7	64.11	927.7	
TOTAL	946		1250667.0	99.47	1322.1	
GRAND TOTAL	955		1257708.0	100.03		

ESTIMATED GRAND MEAN	16.81
TOTAL NUMBER OF OBSERVATIONS	960
NUMBER OF MISSING VALUES	4

ANALYSIS OF VARIANCE

VARIATE: ORGANIC MATTER INTAKE PER EWE (PERIOD 1).

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD. EWES STRATUM					
PAD	3	13253601	86.36	4417867	10.465
RESIDUAL	14 (6)	5910222	38.51	422159	
TOTAL	17	19153808	124.87	1127282	
GRAND TOTAL	17	19163808	124.87		

ESTIMATED GRAND MEAN	1523
TOTAL NUMBER OF OBSERVATIONS	24
NUMBER OF MISSING VALUES	6

TREATMENT

Intake per ewe	500	700	1000	1700
(g OM day^{-1})	773	861	1904	2554

ANALYSIS OF VARIANCE

VARIATE: ORGANIC MATTER INTAKE PER EWE (PERIOD 2)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD.EWES STRATUM					
PAD	3	6625595	96.24	2208531	31.722
RESIDUAL	17 (3)	1183565	17.19	69621	
TOTAL	20	7809160	113.43	390458	
GRAND TOTAL	20	7809160	113.43		

ESTIMATED GRAND MEAN	1216
TOTAL NUMBER OF OBSERVATIONS	24
NUMBER OF MISSING VALUES	3

TREATMENT

Intake per ewe	500	700	1000	1700
(g OM day^{-1})	781	780	1235	2067

ANALYSIS OF VARIANCE

VARIATE: ORGANIC MATTER INTAKE PER LAMB (PERIOD 1)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD. EWES STRATUM					
PAD	3	1172483	116.20	390828	32.111
RESIDUAL	14 (6)	170398	16.89	12171	
TOTAL	17	1342881	133.08	78993	
GRAND TOTAL	17	1342881	133.08		

ESTIMATED GRAND MEAN	537
TOTAL NUMBER OF OBSERVATIONS	24
NUMBER OF MISSING VALUES	6

TREATMENT

Intake per lamb	500	700	1000	1700
(g OM day^{-1})	301	333	736	779

ANALYSIS OF VARIANCE

VARIATE: ORGANIC MATTER INTAKE PER LAMB (PERIOD 2)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD. EWES STRATUM					
PAD	3	2282372	100.70	760791	48.251
RESIDUAL	17 (3)	268044	11.83	15767	
TOTAL	20	2550415	112.53	127521	
GRAND TOTAL	20	2550415	112.53		

ESTIMATED GRAND MEAN	644
TOTAL NUMBER OF OBSERVATIONS	24
NUMBER OF MISSING VALUES	3

TREATMENT

Intake per lamb	500	700	1000	1700
(g OM day^{-1})	326	373	813	1065

ANALYSIS OF VARIANCE

VARIATE: INTAKE PER EWE PLUS LAMB UNIT (PERIOD 1)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD. EWES STRATUM					
PAD	3	22099216	105.73	7366405	19.757
RESIDUAL	14 (6)	5219785	24.97	372842	
TOTAL	17	27318992	130.70	1606999	
GRAND TOTAL	17	27318992	130.70		

ESTIMATED GRAND MEAN 2060
TOTAL NUMBER OF OBSERVATIONS 24
NUMBER OF MISSING VALUES 6

TREATMENT

Intake per ewe + lamb	500	700	1000	1700
(g OM day^{-1})	1074	1192	2641	3333

ANALYSIS OF VARIANCE

VARIATE: INTAKE PER EWE PLUS LAMB UNIT (PERIOD 2)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD. EWES STRATUM					
PAD	3	16323150	104.57	5441050	63.033
RESIDUAL	17 (3)	1467442	9.40	86320	
TOTAL	20	17790592	113.97	889530	
GRAND TOTAL	20	17790592	113.97		

ESTIMATED GRAND MEAN	1860
TOTAL NUMBER OF OBSERVATIONS	24
NUMBER OF MISSING VALUES	3

TREATMENT

Intake per ewe + lamb	500	700	1000	1700
(g OM day^{-1})	1108	1153	2048	3132

ANALYSIS OF VARIANCE

VARIATE: TOTAL ORGANIC MATTER CONSUMPTION PER HECTARE (PERIOD 1)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD. EWES STRATUM					
PAD	3	6.087E 8	34.94	2.029E 8	2.229
RESIDUAL	14 (6)	1.275E 9	73.16	9.104E 7	
TOTAL	17	1.883E 9	108.10	1.108E 8	
GRAND TOTAL	17	1.883E 9	108.10		

ESTIMATED GRAND MEAN	46205
TOTAL NUMBER OF OBSERVATIONS	24
NUMBER OF MISSING VALUES	6

ANALYSIS OF VARIANCE

VARIATE: TOTAL ORGANIC MATTER CONSUMPTION PER HECTARE (PERIOD 2)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
PAD. EWES STRATUM					
PAD	3	2.563E 9	83.80	8.543E 8	21.964
RESIDUAL	17 (3)	6.612E 8	21.62	3.889E 7	
TOTAL	20	3.224E 9	105.42	1.612E 8	
GRAND TOTAL	20	3.224E 9	105.42		

ESTIMATED GRAND MEAN	41020
TOTAL NUMBER OF OBSERVATIONS	24
NUMBER OF MISSING VALUES	3

ANALYSIS OF VARIANCE

VARIATE: GRAZING TIME (PERIOD 1)

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
RECORD STRATUM	9		45.066	42.20	5.007	3.233
RECORD. UNITS STRATUM						
PAD	3		45.578	42.68	15.193	9.808
RESIDUAL	19	(8)	29.430	27.56	1.549	
TOTAL	22		75.008	70.24	3.409	
GRAND TOTAL	31		120.074	112.45		

ESTIMATED GRAND MEAN	11.71
TOTAL NUMBER OF OBSERVATIONS	40
NUMBER OF MISSING VALUES	8

TREATMENT

Grazing Time	500	700	1000	1700
(Hrs)	11.02	13.06	12.40	10.37

ANALYSIS OF VARIANCE

VARIATE: GRAZING TIME (PERIOD 2)

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
RECORD STRATUM	12		139.81	36.15	11.65	1.154
RECORD. UNITS STRATUM						
PAD	3		78.84	20.38	26.28	2.604
RESIDUAL	25	(11)	252.29	65.23	10.09	
TOTAL	28		331.13	85.61	11.83	
GRAND TOTAL	40		470.93	121.76		

ESTIMATED GRAND MEAN	12.52
TOTAL NUMBER OF OBSERVATIONS	52
NUMBER OF MISSING VALUES	11

TREATMENT

Grazing Time	500	700	1000	1700
(Hrs)	11.24	12.75	14.42	11.65

ANALYSIS OF VARIANCE

VARIATE: RATE OF BITING (PERIOD 1)

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
RECORD STRATUM	9	1156.4	11.26	128.5	0.272
RECORD. UNITS STRATUM					
PAD	3	664.1	6.46	221.4	0.468
RESIDUAL	19 (8)	8988.9	87.51	473.1	
TOTAL	22	9653.0	93.97	438.8	
GRAND TOTAL	31	10809.3	105.23		

ESTIMATED GRAND MEAN	86.9
TOTAL NUMBER OF OBSERVATIONS	40
NUMBER OF MISSING VALUES	8

TREATMENT

	500	700	1000	1700
Rate of biting (bites min^{-1})	92.1	84.0	82.0	89.6

ANALYSIS OF VARIANCE

VARIATE: RATE OF BITING (PERIOD 2)

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
RECORD STRATUM	12		6154.7	37.22	512.9	2.274
RECORD. UNITS STRATUM						
PAD	3		13383.0	80.94	4461.0	19.777
RESIDUAL	25	(11)	5639.2	34.10	225.6	
TOTAL	28		19022.2	115.04	679.4	
GRAND TOTAL	40		25176.9	152.27		

ESTIMATED GRAND MEAN	86.7
TOTAL NUMBER OF OBSERVATIONS	52
NUMBER OF MISSING VALUES	11

TREATMENT

Rate of biting	500	700	1000	1700
(bites min^{-1})	88.0	70.5	76.0	112.2

ANALYSIS OF VARIANCE

VARIATE: ORGANIC MATTER DIGESTIBILITY (PERIOD 1)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	15.354	4.04	5.118	0.810
EWES STRATUM	3	50.888	13.39	16.963	2.684
TIME. EWES STRATUM					
PAD	3	275.892	72.59	91.964	14.550
RESIDUAL	6	37.923	9.98	6.321	
TOTAL	9	313.815	82.57	34.868	
GRAND TOTAL	15	380.058	100.00		
GRAND MEAN	78.61				
TOTAL NUMBER OF OBSERVATIONS	16				

TREATMENT

Organic matter digestibility	500	700	1000	1700
(%)	71.89	78.48	81.61	82.45

ANALYSIS OF VARIANCE

VARIATE: ORGANIC MATTER DIGESTIBILITY (PERIOD 2)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	75.32	9.38	25.11	0.529
EWES STRATUM	3	78.75	9.81	26.25	0.553
TIME.EWES STRATUM					
PAD	3	363.65	45.31	121.22	2.553
RESIDUAL	6	284.93	35.50	47.49	
TOTAL	9	648.58	80.80	72.06	
GRAND TOTAL	15	802.66	100.00		

GRAND MEAN 75.5
TOTAL NUMBER OF OBSERVATIONS 16

TREATMENT

Organic matter digestibility	500	700	1000	1700
(%)	67.9	75.1	78.6	80.4

ANALYSIS OF VARIANCE

VARIATE: LIVE GRASS LEAF IN DIET (PERIOD 1)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	107.84	4.86	35.95	1.942
EWES STRATUM	3	118.23	5.32	39.41	2.129
TIME. EWES STRATUM					
PAD	3	1883.69	84.82	627.90	33.917
RESIDUAL	6	111.08	5.00	18.51	
TOTAL	9	1994.76	89.82	221.64	
GRAND TOTAL	15	2220.83	100.00		

GRAND MEAN 79.3
TOTAL NUMBER OF OBSERVATIONS 16

TREATMENT

Live grass leaf	500	700	1000	1700
(%)	61.2	81.8	89.7	84.6

ANALYSIS OF VARIANCE

VARIATE: LIVE GRASS LEAF IN DIET (PERIOD 2)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	131.03	6.62	43.68	0.862
EWES STRATUM	3	335.32	16.95	111.77	2.206
TIME. EWES STRATUM					
PAD	3	1207.45	61.05	402.48	7.942
RESIDUAL	6	304.06	15.37	50.68	
TOTAL	9	1511.50	76.42	167.94	
GRAND TOTAL	15	1977.85	100.00		

GRAND MEAN 74.9
TOTAL NUMBER OF OBSERVATIONS 16

TREATMENT

Live grass leaf	500	700	1000	1700
(%)	60.6	79.6	83.5	75.8

ANALYSIS OF VARIANCE

VARIATE: LIVE PSEUDOSTEM IN DIET (PERIOD 1)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	12.573	3.72	4.191	0.436
EWES STRATUM	3	45.933	13.60	15.311	1.593
TIME. EWES STRATUM					
PAD	3	221.530	65.60	73.843	7.682
RESIDUAL	6	57.674	17.08	9.612	
TOTAL	9	279.204	82.68	31.023	
GRAND TOTAL	15	337.709	100.00		

GRAND MEAN 6.33
TOTAL NUMBER OF OBSERVATIONS 16

TREATMENT

Live pseudostem	500	700	1000	1700
(%)	12.69	5.20	3.58	3.85

ANALYSIS OF VARIANCE

VARIATE: LIVE PSEUDOSTEM IN DIET (PERIOD 2)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	4.100	2.40	1.367	0.705
EWES STRATUM	3	69.121	40.39	23.040	11.890
TIME. EWES STRATUM					
PAD	3	86.302	50.42	28.767	14.846
RESIDUAL	6	11.627	6.79	1.938	
TOTAL	9	97.929	57.22	10.881	
GRAND TOTAL	15	171.149	100.00		

GRAND MEAN 7.53
TOTAL NUMBER OF OBSERVATIONS 16

TREATMENT

Live pseudostem	500	700	1000	1700
(%)	11.17	7.86	5.11	5.99

ANALYSIS OF VARIANCE

VARIATE: DEAD TISSUE IN DIET (PERIOD 1)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	24.37	3.33	8.12	0.469
EWES STRATUM	3	57.88	7.90	19.29	1.113
TIME. EWES STRATUM					
PAD	3	546.56	74.58	182.19	10.511
RESIDUAL	6	104.00	14.19	17.33	
TOTAL	9	650.56	88.78	72.28	
GRAND TOTAL	15	732.81	100.00		

GRAND MEAN 6.0
TOTAL NUMBER OF OBSERVATIONS 16

TREATMENTS

Dead Tissue	500	700	1000	1700
(%)	15.9	4.7	1.3	2.1

ANALYSIS OF VARIANCE

VARIATE: DEAD TISSUE IN DIET (PERIOD 2)

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TIME STRATUM	3	47.597	15.71	15.866	1.843
EWES STRATUM	3	87.437	28.87	29.146	3.385
TIME. EWES STRATUM					
PAD	3	116.214	38.37	38.738	4.500
RESIDUAL	6	51.655	17.05	8.609	
TOTAL	9	167.868	55.42	18.652	
GRAND TOTAL	15	302.903	100.00		

GRAND MEAN 8.30
TOTAL NUMBER OF OBSERVATIONS 16

TREATMENT

Dead Tissue	500	700	1000	1700
(%)	12.34	6.21	5.53	9.13

APPENDIX 5

Table 1 Number daughter tillers (stolons) per primary tiller (stolon).

Treatment	Ryegrass	Poa annua	White clover
LL	0.07 a[1/]	0.18 ab	0.41 a
HH	0.12 a	0.23 ab	0.44 a
LH	0.00 a	0.01 b	0.43 a
HL	0.10 a	0.33 a	0.48 a
	SE = 0.087	LSD = 0.26	

Table 2 Pseudostem (stolon) growth per primary tiller (stolon) in µg DM tiller (stolon)$^{-1}$ day^{-1}.

Treatment	Ryegrass	Poa annua	White clover
LL	10 ab	7 a	1 b
HH	0 c	0 a	0 b
LH	15 a	0 a	12 a
HL	1 bc	0 a	-2 b
	SE = 3.7	LSD = 10.5	

1/ In tables 1-4, values in columns without common lower case letters are significantly ($P<0.05$) different.

Table 3 Net production per primary tiller (stolon) in μg DM tiller (stolon)$^{-1}$ day^{-1}.

Treatment	Ryegrass		Poa annua		White clover	
LL	82	ab	5	a	74	a
HH	141	a	-15	a	76	a
LH	110	ab	38	a	85	a
HL	61	b	- 4	a	28	a

SE = 21.7 LSD = 62

Table 4 Pseudostem (stolon) growth per unit area in kg DM ha^{-1} day^{-1}

Treatment	Ryegrass	Poa annua	White clover
LL	3.5 a	1.3 a	0.0 a
HH	0.0 b	0.0 a	0.0 a
LH	3.7 a	0.0 a	0.1 a
HL	0.1 b	0.0 a	0.0 a

SE = 0.61 LSD = 1.73

A P P E N D I X 6

Analysis of variance tables for experiment 2

1. Data for primary units in ANOVA tables are in mg.

ANALYSIS OF VARIANCE

VARIATE: RYEGRASS POPULATION DENSITY

SOURCE OF VARIATION	DF		SS	SS%		MS	VR
SAMPLE STRATUM	11	1.625E	9	13.84	1.477E	8	1.121
SAMPLE. UNITS STRATUM							
PADDOCKS†	5	2.874E	9	24.47	5.747E	8	4.363
RESIDUAL	55	7.245E	9	61.69	1.317E	8	
TOTAL	60	1.012E	10	86.16	1.686E	8	
GRAND TOTAL	71	1.174E	10	100.00			
GRAND MEAN	24256						
TOTAL NUMBER OF OBSERVATIONS	72						

† Experiment 1 500 and 1000 treatments included.

ANALYSIS OF VARIANCE

VARIATE: POA POPULATION DENSITY

SOURCE OF VARIATION	DF		SS	SS%		MS	VR
SAMPLE STRATUM	11	1.557E	9	16.04	1.416E	8	1.727
SAMPLE. UNITS STRATUM							
PADDOCKS†	5	3.641E	9	37.51	7.282E	8	8.883
RESIDUAL	55	4.509E	9	46.45	8.198E	7	
TOTAL	60	8.150E	9	83.96	1.358E	8	
GRAND TOTAL	71	9.707E	9	100.00			
GRAND MEAN		13914					
TOTAL NUMBER OF OBSERVATIONS		72					

† Experiment 1 500 and 1000 treatments included.

ANALYSIS OF VARIANCE

VARIATE: CLOVER POPULATION DENSITY

SOURCE OF VARIATION	DF		SS	SS%		MS	VR
SAMPLE STRATUM	11	1.790E	8	12.44	1.627E	7	0.785
SAMPLE. UNITS STRATUM							
PADDOCKS †	5	1.202E	8	8.36	2.405E	7	1.61
RESIDUAL	55	1.139E	9	79.20	2.072E	7	
TOTAL	60	1.260E	9	87.56	2.100E	7	
GRAND TOTAL	71	1.439E	9	100.00			
GRAND MEAN		1397					
TOTAL NUMBER OF OBSERVATIONS		72					

† Experiment 1 500 and 1000 treatments included.

ANALYSIS OF VARIANCE

VARIATE: TOTAL POPULATION DENSITY

SOURCE OF VARIATION	DF		SS	SS%		MS	VR
SAMPLE STRATUM	11	1.679E	9	6.93	1.526E	8	0.848
SAMPLE. UNITS STRATUM							
PADDOCKS†	5	1.267E	10	52.25	2.534E	9	14.081
RESIDUAL	55	9.896E	9	40.82	1.799E	8	
TOTAL	60	2.256E	10	93.07	3.761E	8	
GRAND TOTAL	71	2.424E	10	100.00			
GRAND MEAN		43003					
TOTAL NUMBER OF OBSERVATIONS		72					

† Experiment 1 500 and 1000 treatments included.

ANALYSIS OF VARIANCE

VARIATE: LEAF AREA PER PRIMARY UNIT

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.0437	0.01	0.0437	0.139
TRANSECT. TILLER STRATUM	8	4.6932	1.49	0.5866	1.864
TRANSECT. TILLER. UNITS STRATUM					
SPECIES	2	3.3863	1.08	1.6932	5.380
PADDOCK	3	141.5165	45.08	47.1722	149.879
QUARTER	3	2.7178	0.87	0.9059	2.878
SPECIES. PADDOCK	6	15.9517	5.08	2.6586	8.447
SPECIES. QUARTER	6	2.5152	0.80	0.4192	1.332
PADDOCK. QUARTER	9	3.7417	1.19	0.4157	1.321
SPECIES. PADDOCK. QUARTER	18	6.2483	1.99	0.3471	1.103
RESIDUAL	423	133.1333	42.41	0.3147	
TOTAL	470	309.2109	98.49	0.6579	
GRAND TOTAL	479	313.9478	100.00		

GRAND MEAN 0.877
TOTAL NUMBER OF OBSERVATIONS 480

ANALYSIS OF VARIANCE

VARIATE: LEAF AREA INDEX

SOURCE OF VARIATION	DF	SS	SS%	MS	VR
TRANSECT STRATUM	1	1.9767	0.17	1.9767	2.843
TRANSECT. TILLER STRATUM	8	8.1246	0.71	1.0156	1.461
TRANSECT. TILLER. UNITS STRATUM					
SPECIES	2	365.3159	31.84	182.6580	262.688
PADDOCK	3	241.9124	21.08	80.6375	115.968
QUARTER	3	7.1266	0.62	2.3755	3.416
SPECIES. PADDOCK	6	184.8343	16.11	30.8057	44.303
SPECIES. QUARTER	6	11.4118	0.99	1.9020	2.735
PADDOCK. QUARTER	9	12.2540	1.07	1.3616	1.958
SPECIES. PADDOCK. QUARTER	18	20.2454	1.76	1.1247	1.618
RESIDUAL	423	294.1301	25.64	0.6953	
TOTAL	470	1137.2300	99.12	2.4196	
GRAND TOTAL	479	1147.3311	100.00		

GRAND MEAN 1.034
TOTAL NUMBER OF OBSERVATIONS 480

ANALYSIS OF VARIANCE

VARIATE: NUMBER OF DAUGHTERS PER PRIMARY UNIT

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		0.4189	0.24	0.4189	1.263
TRANSECT. TILLERS STRATUM	8		0.6398	0.37	0.0800	0.241
TRANSECT. TILLERS. UNITS STRATUM						
SPECIES	2		11.2626	6.47	5.6313	16.976
PADDOCKS	3		1.6152	0.93	0.5384	1.623
QUARTERS	3		2.6281	1.51	0.8760	2.641
SPECIES. PADDOCKS	6		1.0652	0.61	0.1775	0.535
SPECIES. QUARTERS	6		8.0444	4.62	1.3407	4.042
PADDOCKS. QUARTERS	9		2.3566	1.35	0.2618	0.789
SPECIES. PADDOCKS. QUARTERS	18		6.9527	3.99	0.3863	1.164
RESIDUAL	421	(2)	139.6572	80.17	0.3317	
TOTAL	468		173.5820	99.65	0.3709	
GRAND TOTAL	477		174.6407	100.26		

ESTIMATED GRAND MEAN	0.233
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: LAMINA GROWTH PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.000469	0.01	0.000469	0.054
TRANSECT. TILLERS STRATUM	8	0.068181	1.17	0.008523	0.977
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	0.445369	7.66	0.222685	25.518
PADDOCKS	3	0.965622	16.60	0.321874	36.884
QUARTERS	3	0.033053	0.57	0.011018	1.263
SPECIES. PADDOCKS	6	0.386181	6.64	0.064363	7.376
SPECIES. QUARTERS	6	0.114749	1.97	0.019125	2.192
PADDOCKS. QUARTERS	9	0.026370	0.45	0.002930	0.336
SPECIES. PADDOCKS. QUARTERS	18	0.106774	1.84	0.005932	0.680
RESIDUAL	421 (2)	3.673903	63.16	0.008727	
TOTAL	468	5.752017	98.89	0.012291	
GRAND TOTAL	477	5.820666	100.07		

ESTIMATED GRAND MEAN	0.1271
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: PSEUDOSTEM (STOLON) GROWTH PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.0025573	0.92	0.0025573	4.699
TRANSECT. TILLERS STRATUM	8	0.0027007	0.97	0.0003376	0.620
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	0.0019157	0.69	0.0009578	1.760
PADDOCKS	3	0.0074353	2.67	0.0024784	4.554
QUARTERS	3	0.0004725	0.17	0.0001575	0.289
SPECIES. PADDOCKS	6	0.0048954	1.76	0.0008159	1.499
SPECIES. QUARTERS	6	0.0084544	3.04	0.0014091	2.589
PADDOCKS. QUARTERS	9	0.0109242	3.92	0.0012138	2.230
SPECIES. PADDOCKS. QUARTERS	18	0.0116682	4.19	0.0006482	1.91
RESIDUAL	421 (2)	0.2291198	82.28	0.0005442	
TOTAL	468	0.2748856	98.71	0.0005874	
GRAND TOTAL	477	0.2801436	100.60		

ESTIMATED GRAND MEAN	0.0037
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: TOTAL GROWTH PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.000836	0.01	0.000836	0.086
TRANSECT. TILLERS STRATUM	8	0.087560	1.35	0.010945	1.122
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	0.498422	7.69	0.249211	25.552
PADDOCKS	3	1.052493	16.25	0.350831	35.971
QUARTERS	3	0.032281	0.50	0.010760	1.103
SPECIES. PADDOCKS	6	0.425238	6.56	0.070873	7.267
SPECIES. QUARTERS	6	0.104543	1.61	0.017424	1.786
PADDOCKS. QUARTERS	9	0.051320	0.79	0.005702	0.585
SPECIES. PADDOCKS. QUARTERS	18	0.129146	1.99	0.007175	0.736
RESIDUAL	421 (2)	4.106123	63.39	0.009753	
TOTAL	468	6.399564	98.79	0.013674	
GRAND TOTAL	477	6.487959	100.16		

ESTIMATED GRAND MEAN	0.1307
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: LAMINA SENESCENCE PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.007186	0.12	0.007186	0.724
TRANSECT. TILLERS STRATUM	8	0.051967	0.90	0.006496	0.655
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	0.019028	0.33	0.009514	0.959
PADDOCKS	3	0.469234	8.13	0.156411	15.763
QUARTERS	3	0.131495	2.28	0.043832	4.417
SPECIES. PADDOCKS	6	0.466968	8.09	0.077828	7.844
SPECIES. QUARTERS	6	0.091179	1.58	0.015196	1.532
PADDOCKS. QUARTERS	9	0.225712	3.91	0.025079	2.528
SPECIES. PADDOCKS. QUARTERS	18	0.141843	2.46	0.007880	0.794
RESIDUAL	421 (2)	4.177360	72.41	0.009922	
TOTAL	468	5.722817	99.20	0.012228	
GRAND TOTAL	477	5.781970	100.23		

ESTIMATED GRAND MEAN	-0.0740
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: NET PRODUCTION PER PRIMARY UNIT

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.01292	0.13	0.01292	0.686
TRANSECT. TILLERS STRATUM	8	0.08044	0.82	0.01005	0.534
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	0.70456	7.22	0.35228	18.695
PADDOCKS	3	0.16442	1.68	0.05481	2.909
QUARTERS	3	0.15009	1.54	0.05003	2.655
SPECIES. PADDOCKS	6	0.12346	1.26	0.02058	1.092
SPECIES. QUARTERS	6	0.20843	2.14	0.03474	1.844
PADDOCKS. QUARTERS	9	0.18229	1.87	0.02025	1.075
SPECIES. PADDOCKS. QUARTERS	18	0.23575	2.42	0.01310	0.695
RESIDUAL	421 (2)	7.93312	81.28	0.01884	
TOTAL	468	9.70212	99.40	0.02073	
GRAND TOTAL	477	9.79547	100.36		

ESTIMATED GRAND MEAN	0.0568
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: LAMINA GROWTH PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	175.0	0.07	175.0	0.717
TRANSECT. TILLERS STRATUM	8	1005.0	0.39	125.6	0.515
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	113384.4	43.72	56692.2	232.288
PADDOCKS	3	18266.5	7.04	6088.8	24.948
QUARTERS	3	899.8	0.35	299.9	1.229
SPECIES. PADDOCKS	6	15568.2	6.00	2594.7	10.631
SPECIES. QUARTERS	6	1920.9	0.74	320.1	1.312
PADDOCKS. QUARTERS	9	1775.0	0.68	197.2	0.808
SPECIES. PADDOCKS. QUARTERS	18	3908.9	1.51	217.2	0.890
RESIDUAL	421 (2)	102749.1	39.62	244.1	
TOTAL	468	258472.6	99.67	552.3	
GRAND TOTAL	477	259652.6	100.13		

ESTIMATED GRAND MEAN	16.02
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: PSEUDOSTEM (STOLON) GROWTH PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	0.76	0.01	0.76	0.052
TRANSECT. TILLERS STRATUM	8	83.96	1.05	10.49	0.713
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	294.33	3.68	147.16	9.996
PADDOCKS	3	252.19	3.15	84.06	5.710
QUARTERS	3	140.33	1.75	46.78	3.177
SPECIES. PADDOCKS	6	307.38	3.84	51.23	3.480
SPECIES. QUARTERS	6	203.79	2.55	33.97	2.307
PADDOCKS. QUARTERS	9	173.21	2.16	19.25	1.307
SPECIES. PADDOCKS. QUARTERS	18	352.36	4.40	19.58	1.330
RESIDUAL	421 (2)	6198.14	77.45	14.72	
TOTAL	468	7921.73	98.99	16.93	
GRAND TOTAL	477	8006.44	100.05		

ESTIMATED GRAND MEAN	0.72
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: TOTAL GROWTH PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	151.0	0.05	151.0	0.565
TRANSECT. TILLERS STRATUM	8	1354.3	0.47	169.3	0.633
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	125028.4	43.57	62514.2	233.659
PADDOCKS	3	21361.0	7.44	7120.3	26.614
QUARTERS	3	1115.6	0.39	371.9	1.390
SPECIES. PADDOCKS	6	17891.7	6.24	2982.0	11.146
SPECIES. QUARTERS	6	1318.9	0.46	219.8	0.822
PADDOCKS. QUARTERS	9	2120.7	0.74	235.6	0.881
SPECIES. PADDOCKS. QUARTERS	18	4360.7	1.52	242.3	0.905
RESIDUAL	421 (2)	112636.3	39.26	267.5	
TOTAL	468	285833.2	99.62	610.8	
GRAND TOTAL	477	287338.5	100.14		

ESTIMATED GRAND MEAN	16.76
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: LAMINA SENESCENCE PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	1.6	0.00	1.6	0.009
TRANSECT. TILLERS STRATUM	8	881.3	0.72	110.2	0.584
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	17296.4	14.19	8648.2	45.850
PADDOCKS	3	6498.3	5.33	2166.1	11.484
QUARTERS	3	2169.6	1.78	723.2	3.834
SPECIES. PADDOCKS	6	5692.3	4.67	948.7	5.030
SPECIES. QUARTERS	6	2750.3	2.26	458.4	2.430
PADDOCKS. QUARTERS	9	3015.5	2.47	335.1	1.776
SPECIES. PADDOCKS. QUARTERS	18	4272.2	3.50	237.3	1.258
RESIDUAL	421 (2)	79407.8	65.13	188.6	
TOTAL	468	121102.3	99.33	258.8	
GRAND TOTAL	477	121985.3	100.06		

ESTIMATED GRAND MEAN	-7.79
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: NET PRODUCTION PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	183.9	0.06	183.9	0.381
TRANSECT. TILLERS STRATUM	8	1790.8	0.62	223.8	0.464
TRANSECT. TILLERS. UNITS STRATUM					
SPECIES	2	52514.6	18.18	26257.3	54.431
PADDOCKS	3	5243.0	1.81	1747.7	3.623
QUARTERS	3	2889.9	1.00	963.3	1.997
SPECIES. PADDOCKS	6	7074.0	2.45	1179.0	2.444
SPECIES. QUARTERS	6	4991.2	1.73	831.9	1.724
PADDOCKS. QUARTERS	9	4278.3	1.48	475.4	0.985
SPECIES. PADDOCKS. QUARTERS	18	7058.3	2.44	392.1	0.813
RESIDUAL	421 (2)	203086.9	70.30	482.4	
TOTAL	468	287136.1	99.40	613.5	
GRAND TOTAL	477	289110.8	100.08		

ESTIMATED GRAND MEAN	9.0
TOTAL NUMBER OF OBSERVATIONS	480
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: COMBINED SPECIES TOTAL GROWTH PER UNIT AREA

SOURCE OF VARIATION	DF	(MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1		522.1	0.28	522.1	0.624
TRANSECT. TILLERS STRATUM	8		4100.0	2.19	512.5	0.613
TRANSECT. TILLERS. UNITS STRATUM						
PADDOCKS	3		62797.6	33.52	20932.5	25.035
QUARTERS	3		3534.8	1.89	1178.3	1.409
PADDOCKS. QUARTERS	9		6215.6	3.32	690.6	0.826
RESIDUAL	133	(2)	111206.2	59.36	836.1	
TOTAL	148		183754.1	98.09	1241.6	
GRAND TOTAL	157		188376.2	100.55		

ESTIMATED GRAND MEAN	50.4
TOTAL NUMBER OF OBSERVATIONS	160
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: COMBINED SPECIES LAMINA SENESCENCE PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	4.4	0.00	4.4	0.008
TRANSECT. TILLERS STRATUM	8	2728.7	2.39	341.1	0.592
TRANSECT. TILLERS. UNITS STRATUM					
PADDOCKS	3	19749.7	17.27	6583.2	11.428
QUARTERS	3	6350.7	5.55	2116.9	3.675
PADDOCKS. QUARTERS	9	9143.9	7.99	1016.0	1.764
RESIDUAL	133 (2)	76619.4	66.99	576.1	
TOTAL	148	111863.7	97.81	755.8	
GRAND TOTAL	157	114596.8	100.20		

ESTIMATED GRAND MEAN	-23.4
TOTAL NUMBER OF OBSERVATIONS	160
NUMBER OF MISSING VALUES	2

ANALYSIS OF VARIANCE

VARIATE: COMBINED SPECIES NET PRODUCTION PER UNIT AREA

SOURCE OF VARIATION	DF (MV)	SS	SS%	MS	VR
TRANSECT STRATUM	1	622	0.25	622	0.409
TRANSECT. TILLERS STRATUM	8	5787	2.36	723	0.475
TRANSECT. TILLERS. UNITS STRATUM					
PADDOCKS	3	14674	5.99	4891	3.210
QUARTERS	3	8507	3.47	2836	1.861
PADDOCKS. QUARTERS	9	13104	5.35	1456	0.956
RESIDUAL	133 (2)	202634	82.76	1524	
TOTAL	148	238919	97.58	1614	
GRAND TOTAL	157	245328	100.20		

ESTIMATED GRAND MEAN	27.0
TOTAL NUMBER OF OBSERVATIONS	160
NUMBER OF MISSING VALUES	2

APPENDIX 7

The texts of four conference papers which utilise data presented in this thesis.

1. Paper presented to a 'Workshop on Mixed Grazing' in Galway, Ireland, sponsored by the Agricultural Institutes of Ireland and Iceland; 1980.

2. Paper presented to the 'XIV International Grassland Congress', Lexington, U.S.A., 1981.

3. & 4. Papers presented to a Symposium on 'Plant Physiology and Herbage Production' sponsored by the British Grassland Society, Nottingham, 1981.

Herbage Mass and Height : Their Relevance to Management Systems

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Introduction

Mixed cattle and sheep grazing can be advantageous in production terms compared to single species grazing (Connolly and Nolan, 1976) and the mechanisms of this response are not only of considerable interest but also of economic importance in that they may point the way to more efficient and productive systems of management.

In most experiments where higher output per unit area to mixed species stocking has been observed, the advantage has been attributed to better sheep performance through improved utilisation of herbage resultant from the sheep eating herbage which steers in particular had refused (Nolan and Connolly, 1977) although other factors, e.g. differences in grazing habit and reduced gastrointestinal round worm

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burden in sheep, have also been implicated.

In this paper, some aspects of herbage production under sheep and cattle grazing, alone and mixed, will be discussed.

The Components of Herbage Production

Herbage production in grazing experiments is usually estimated as the difference between successive measurements of herbage mass and as such is strictly an estimate of net production (NP), the balance between growth (G) and loss to senescence and decomposition (S). All are expressed as rates (kg/ha/unit time):

$$NP = G - S \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 1$$

This definition is sufficient in the absence of the grazing animal, but when the animal is present it becomes inadequate. In such circumstances any net change in herbage mass, defined as net herbage accumulation (NHA), represents the balance between the rates of growth (G), and senescence losses (S) and consumption (C):

$$NHA = NP - C = G - (S + C) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 2$$

Further, in a continuously grazed sward maintained in a steady state net accumulation is zero.

$$\text{Then:} \quad G - (S + C) = 0$$

$$\therefore \quad G - S = C \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 3$$

and NP as defined in Equation 1 is equal to C.

The results of a recent grazing study conducted at the Hill Farming Research Organisation are used to illustrate the influence of sward conditions upon the components of herbage production, and the balance between them. This provides a basis for discussion of the implications of the results of mixed stocking experiments, and the procedures for examining sward responses to variations in grazing management.

In this experiment, a mixed species sward (perennial ryegrass, Poa, white clover association) was maintained in as near steady state as possible at four different levels of herbage mass by continuous but variable stocking with ewes and lambs, so that net herbage accumulation was zero. The range of herbage mass and the equivalent range of sward height are shown in Figure 1. The technique used to determine growth, senescence and net production involved measurement of tissue gains and losses on individual plant units (tillers or stolons) and the populations of the plant units. The product of tissue changes per unit and unit populations gave estimates of growth and senescence per unit area for individual species and for the sward as a whole. To obtain the necessary information, laminae or petiole lengths, leaf areas and pseudostem or stolon lengths were measured on 5 occasions over periods of 2 weeks and converted into weights from a knowledge of weight/length and weight/area ratios.

The results (Figure 1) show that herbage growth rate increased to an asymptote (118 kg DM/ha/day), and the rate of senescence

increased linearly with increasing herbage mass and height, so that the rate of net production (NP, equation 1) increased to a maximum and then decreased (Figure 1).

Cattle versus Sheep

Cattle swards have been observed to have lower rates of net production than sheep swards (Boswell, 1976; Monteath, Johnstone and Boswell, 1977) although the reverse has also been reported (Joyce, 1970).

Swards grazed by cattle frequently have areas of high herbage mass and height surrounding dung patches which are not apparent on many swards grazed by sheep alone. It is therefore probably reasonable to suggest that overall the herbage mass present on such cattle swards is higher than that present on sheep swards, and the results of Joyce (1970) may well have been due to the accrued benefits of more lenient summer grazing in a summer dry region (Brougham, 1970). However, if the assumption about the relative heights of cattle and sheep grazed swards is reasonable, then net production on cattle swards may be higher or lower than that on sheep swards, depending upon their position on the response curve shown in Figure 1. The lower rates of net production observed by Boswell (1976) and Monteath, Johnstone and Boswell (1977) on cattle grazed swards would be explained by a relatively high rate of

senescence loss rather than a lower herbage growth rate.

Conversely, in a rotational grazing system if sward heights and herbage masses before grazing are similar for both cattle and sheep grazed swards, and the efficiencies of utilisation (herbage consumed/herbage mass prior to grazing) achieved are similar, then similar levels of net production would be expected. Under such circumstances, Boswell and Cranshaw (1978) reported similar net production rates for swards grazed by sheep and cattle alone (Table 1).

In the same experiment, Boswell and Cranshaw (1978) found that estimates of net production and of herbage utilisation were higher on their mixed cattle and sheep grazed swards than on swards grazed by sheep or cattle alone. Since the swards were similar before grazing, differences in utilisation mean differences in the amount of herbage remaining after grazing, and in a rotational grazing system much of this residual tissue must eventually die. Then, even if the growth rates of all the swards were similar, (and this seems likely because herbage mass and sward height before grazing were similar for all treatments), different rates of net production would be expected (Equation 1 and Figure 1). Therefore, the reported differences in net production between swards grazed by cattle and sheep alone and together (Boswell and Cranshaw, 1978) could well be functions of the different efficiencies of utilisation rather than of differences in herbage growth.

The relevance of equations 1-3 in describing herbage production under grazing can now be appreciated.

Experimental Techniques

Several points relevant to the study of mixed cattle and sheep grazing systems emerge. It is obvious that the cyclic interactions that are an integral part of grazing systems make interpretation extremely difficult unless some parts of the system are rigorously controlled.

Under rotational grazing, net production functions of similar form to that depicted in Figure 1 are well established for the regrowth phase of pasture (Noy-Meir, 1975), and it is probable that growth and senescence functions during regrowth are also similar to those depicted in Figure 1. Clearly it is essential that herbage height and mass before grazing be similar across treatments and that similar utilisations be achieved if net production measurements only are to be used and to be interpretable. To achieve utilisations comparable to that obtained on their mixed sheep and cattle treatments, it is likely that Boswell and Cranshaw (1978) would have found it necessary to increase stock numbers on their sheep and cattle only treatments, thus increasing gain per unit area on these treatments. Under continuous stocking, control of the system is more difficult but just as essential if interpretable results are to be obtained. Herbage height and mass must be maintained in as

near the same steady state as possible on all treatments (i.e. variable stock numbers), thus ensuring similar efficiencies of grazing (consumption/growth) if estimates of net production are to be obtained from estimates of consumption per unit area (Equation 3).

If herbage weight and height are allowed to drift in either rotational or continuous stocking systems of management, then herbage growth, senescence and consumption must be measured if the results are to be interpreted. Clearly, simple stocking rate experiments are inadequate for this purpose, and experiments in which the swards are carefully controlled will be necessary. Measurements of the components of herbage production, particularly when combined with information on herbage consumption, allow a clearer understanding of the inter-relationships between the components of the production process, and a better basis for assessment of the scope for further improvement in the efficiency of grazing systems.

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Table 1.* Net production and utilisation for swards grazed by sheep and cattle alone and together.

Treatment		Net Herbage Production	Herbage Utilisation†
Sheep	Cattle	kg DM/ha/year	%
100%	0	11 100	53.9
0	100%	10 900	51.2
34%	66%	13 100	63.2
67%	34%	13 500	65.4

* Adapted from Boswell and Cranshaw (1978).

† Herbage consumed during grazing ÷ herbage present prior to grazing.

Figure 1

Effect of herbage weight (HW) on growth (G), senescence (S), net production (NP) and clover contribution to net accumulation under continuous sheep stocking in summer. All parameters expressed in kg DM/ha/day except herbage weight - kg OM/ha.

Growth

$$G = 118 - \frac{21749480}{HW^2}$$

$P = 0.00008 \qquad R^2 = 0.94$

Senescence

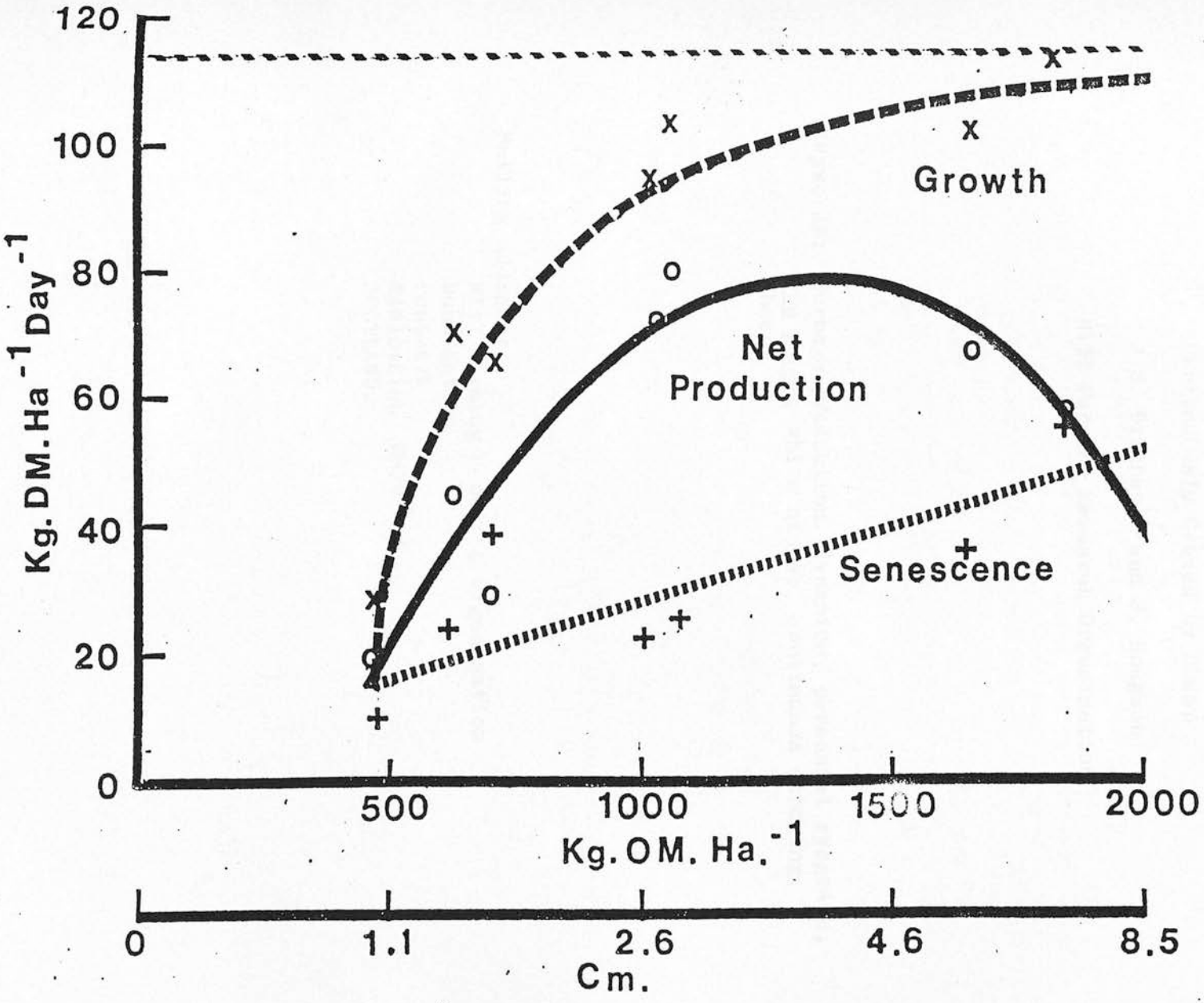
$$S = 7.6 + 0.020\ HW$$

$P = 0.03 \qquad R^2 = 0.56$

Net production

$$NP = 0.28\ HW - 0.00011\ HW^2 - 97.61$$

$P = 0.003 \qquad R^2 = 0.96$


120
100
80
60
40
20
0
Kg. DM. Ha^{-1} Day^{-1}
Growth
Net
Production
Senescence
500
1000
1500
2000
Kg. OM. Ha.$^{-1}$
0
1.1
2.6
4.6
8.5
Cm.

The Dynamics of Herbage Growth and Senescence in a Mixed-Species Temperate Sward Continuously Grazed by Sheep

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Keywords: Herbage production, dynamics, perennial ryegrass, Poa annua, white clover, continuous stocking, sheep

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Four perennial ryegrass (Lolium perenne L.), Poa annua L., white clover (Trifolium repens L.) swards with herbage mass ranging from 500 to 1700 kg OM/ha were established and maintained in as near steady state as possible by continuous but variable stocking with sheep in order to study the influence of herbage mass on rates of herbage growth (G), senescence (S) and net production (NP), and on species balance. Estimates of G, S and NP were derived from measurements on individual grass tillers and clover stolon growth sites.

The mean contributions to total G were 54, 20 and 4 (± 1.6) kg DM $ha^{-1}day^{-1}$ for ryegrass, Poa and clover respectively. The low clover growth rates were due to low population densities, and Poa had lower population densities and lower individual tiller growth rates than ryegrass. The ratio of senescence to growth was 0.47, 0.32 and 0.11 for Poa, ryegrass and clover respectively.

The combined species G increased with herbage mass in an asymptotic manner towards a maximum of 118 kg DM $ha^{-1}day^{-1}$ and S increased linearly from 17 kg $ha^{-1}day^{-1}$ at 500 kg DM ha^{-1} to 41 kg at 1700 kg OM ha^{-1}. NP increased rapidly to a predicted maximum of 70 kg DM $ha^{-1}day^{-1}$ at 1230 kg OM ha^{-1} and then declined slowly.

The results of this experiment suggest that there is limited scope, within practicable limits, for improving rates of net herbage production in temperate swards by manipulation of the herbage mass maintained under continuous stocking management.

Key words: Herbage production, dynamics, perennial ryegrass, Poa annua, white clover, continuous stocking, sheep

3.

Introduction

The control of frequency and severity of defoliation in grazing systems has long been advocated as a means by which both animal and pasture production can be increased, but annual net herbage accumulation in temperate grasslands appears to be relatively insensitive to variations in grazing management or stocking rate (Hodgson and Wade, 1978). Change in the amount of aerial plant tissue is a dynamic process involving the growth of new tissue (G) and the loss of old tissue by decay and decomposition (D), the balance between the two determining net gain or loss (net production, NP). All three can be measured as rates over time on a unit area or an individual plant unit (e.g. a grass tiller) basis. Since management of defoliation can influence both G and D on individual plant units, and also plant population density (Hodgson and Wade, 1978), it is not surprising that there is no general agreement about the effects of grazing management on NP.

The objectives of this study were to investigate the influence of sward conditions under a continuous stocking management on (a) plant growth and senescence and (b) the balance between the main constituents of a mixed species sward. In grazed swards, net herbage accumulation (NHA) is the balance between NP and the consumption of tissue by grazing animals (C):

$$NHA = NP - C = G - (D + C) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

4.

The universal measure of herbage production is net change in herbage mass in the absence of the grazing animal, where C = 0 and therefore NHA = NP. The procedure used here was to maintain swards in as near steady state as possible by continuous but variable stocking with sheep so that NHA = 0 and NP = C. The measurement of D is not easy, and the alternative adopted was to measure senescence (S), the rate of transfer of tissue from the live to the dead state:

$$NP = G - S = C \quad \ldots\ldots\ldots\

laboratory, a stolon growing point being defined as an aggregation of petioles associated with a site of active stolon formation.

Estimates of G, S and NP corrected for tissue removed by defoliation were derived from twice-weekly linear measurements on grass lamina or clover petiole, grass pseudostem or clover stolon, and reproductive stem made over two weeks on 40 individually identified primary or primary + daughter aggregate units per species in each paddock. Measurements were made once in June and once in July. The primary unit for grass was an independent rooted tiller and a dependent attached tiller was the daughter unit. For clover, the primary unit was the terminal growing point of the main stolon and any axillary growing points were daughter units. Constants for weight per unit area and unit length of lamina, pseudostem, petiole and stolon, derived from measurements on randomly selected plant units in each period, were used to convert area and length measurements into estimates of mass. Estimates of G, S and NP were obtained by multiplying unit values for each species by the population density of primary units.

Results

Estimates of total sward G, S and NP in June and July did not differ significantly, so pooled results are shown in Table 1 and Figure 1.

The levels of herbage mass achieved during the experiment were within ± 100 kg OM ha^{-1} of the desired mean levels and

corresponded to the sward height and leaf area index values shown in Figure 1. Species population densities are shown in Table 1. The mean proportion (% dry weight) of ryegrass in the swards increased (33-51%) whereas that of Poa decreased (54-24%) with increasing herbage mass. The mean proportion of clover was 7%, inclusive of stolon tissue, and there was no consistent trend across treatments.

The contributionsto estimates of total sward G (kg DM ha^{-1} day^{-1}) were in the order ryegrass > Poa > clover and estimates of species NP followed the same order (Table 1). Ryegrass G increased with increasing herbage mass up to 1000 kg OM ha^{-1} and then remained constant, whereas Poa G was highest in the 700 kg OM ha^{-1} sward. Highest NP for both ryegrass and Poa occurred at 1000 kg OM ha^{-1}. Clover G and NP were relatively low and showed no consistent trends across treatments.

Fitted functions for the regressions of the combined species estimates of G and S on herbage mass are shown in Figure 1. The increase in G was asymptotic, approaching a maximum of 118 kg DM $ha^{-1}day^{-1}$, and S increased linearly over the full range of herbage mass. The fitted NP curve, combining the functions for G and S, increased to a maximum of 70 kg DM $ha^{-1}day^{-1}$ at a herbage mass of 1230 kg OM ha^{-1} and then fell slowly.

Discussion

Stability was maintained in all except the 500 kg OM ha^{-1}

sward, where uprooted grass tillers comprised a significant proportion of the animal's diet. This effect would exacerbate the decline in estimates of G and NP shown in Table 1 and Figure 1 for that sward which are derived from surviving tillers and stolons.

The differences in G, S and NP between the three species can be explained in terms of species morphology, canopy structure and population density. The tips of the penultimate youngest Poa laminae were subtended below the tips of the corresponding ryegrass laminae on all swards, so lower individual tiller photosynthetic capacities (Woledge, 1978) and growth rates would be expected for Poa than for ryegrass. As herbage mass increased beyond 700 kg OM ha^{-1} ryegrass became the dominant species, and it made the major contribution to NP on all swards. The very low overall contribution of clover was due primarily to its low population density. The higher overall ratio of S to G for Poa (0.47) than for ryegrass (0.32) reflected the relatively low proportion of Poa lamina consumed, which was directly attributable to the position of Poa leaf in the canopy. Most of the clover laminae were subtended into the grazed horizon and defoliated, leaving only petiole tissue to senesce, so the overall ratio of S to G was only 0.11.

Population density and NP per unit were both severely depressed below 700 kg OM ha^{-1}. The rate of increase in individual tiller and stolon NP exceeded the rate of decline in

population density between 700 and 1000 kg OM ha^{-1}, but both NP per unit and population density tended to decline with further increase in herbage mass. The balance between the changes in population density and in the rates of G and S for the individual units of production meant that the predicted NP was equal to 90% or more of maximum over a range of herbage mass from 850 to 1950 kg OM ha^{-1}. These results support the hypothesis that there is limited scope, within practicable limits, for influencing rates of net herbage production in temperate swards by manipulation of the herbage mass maintained under continuous stocking management.

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Footnotes

[1] On study leave from Whatawhata Hill Country Research Station, Hamilton, New Zealand.

11.

Figure Titles

Fig. 1. Combined species growth (G), senescence (S) and net production (NP) rates (kg DM $ha^{-1}day^{-1}$) versus herbage mass (HM), sward surface height and leaf area index.

$$G = 118\ (\pm 5.4) - \frac{21749480\ (\pm 2313000)}{HM^2} \quad R^2 = 0.94^{***},\ n = 8$$

$$S = 7\ (\pm 7.9) + 0.02\ (\pm 0.007)\ HM \quad R^2 = 0.56^{*},\ n = 8$$

$$NP = 113\ (\pm 29.1) - 0.02\ (\pm 0.02)\ HM - \frac{21435530\ (\pm 6188800)}{HM^2}$$

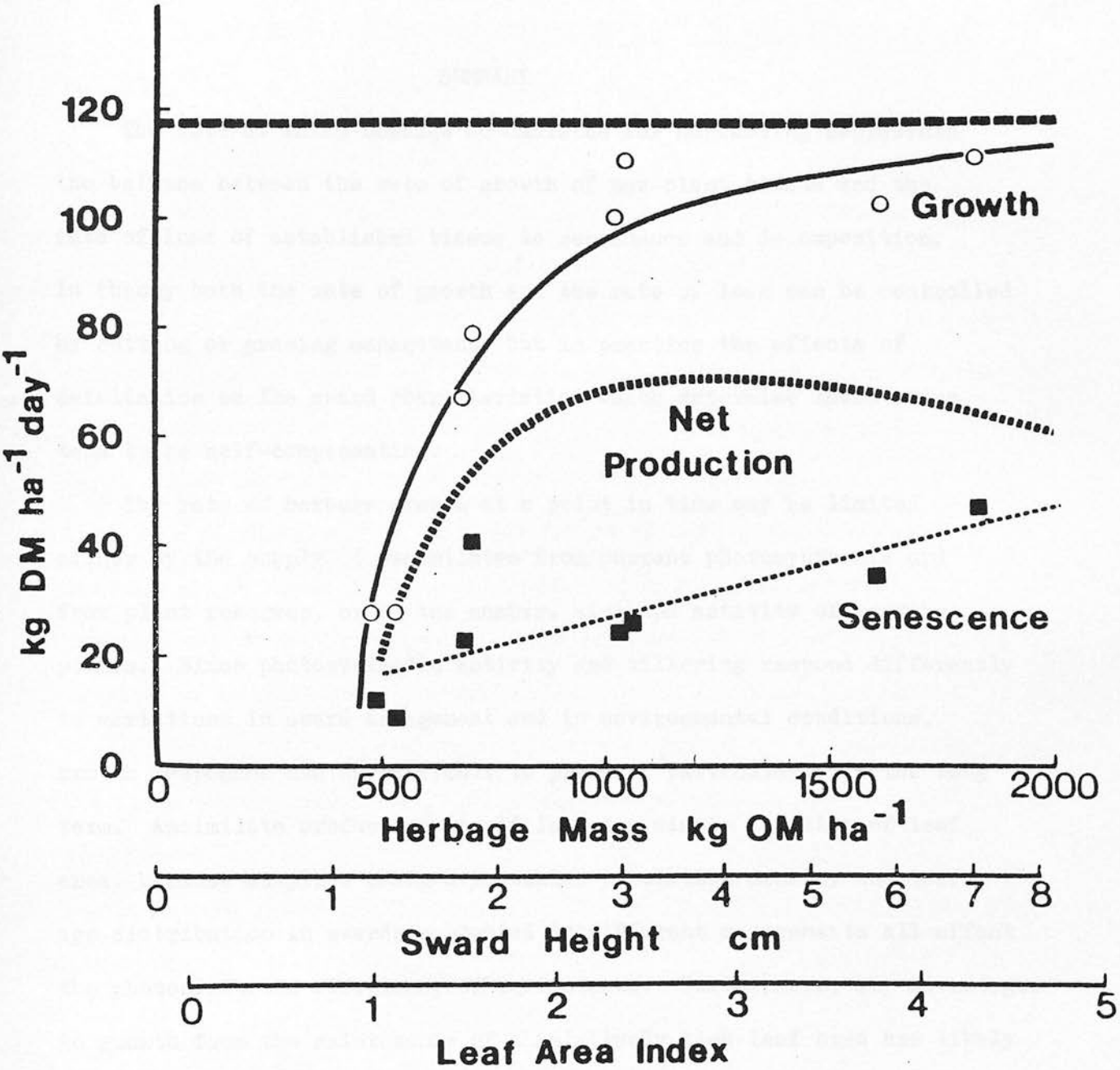
$$R^2 = 0.83^{**},\ n = 8$$

12.

Table 1. Population density (units m^{-2}) and rates of growth, senescence and net production (kg DM $ha^{-1}day^{-1}$) of herbage in continuously stocked swards.

	Treatment				
	500	700	1000	1700	S.E.
Population Density (units m^{-2})					
Ryegrass	14300 b†	28900 a	24700 a	20900 ab	2640
Poa	11900 b	21500 a	10800 b	8900 b	2690
Clover	1400 a	1000 a	700 a	1100 a	570
Growth (kg DM $ha^{-1}day^{-1}$)					
Ryegrass	17 d	40 b	80 a	79 a	3.1
Poa	7 e	30 c	24 cd	19 d	
Clover	4 e	3 e	3 e	5 e	
Senescence (kg DM $ha^{-1}day^{-1}$)					
Ryegrass	6 c	14 b	17 b	32 a	1.9
Poa	4 cd	18 b	7 c	9 c	
Clover	0.2 d	0.3 d	0.1 d	0.8 d	
Net Production (kg DM $ha^{-1}day^{-1}$)					
Ryegrass	11 de	26 c	63 a	47 b	3.4
Poa	4 ef	12 de	16 d	11 de	
Clover	4 ef	2 f	3 ef	4 ef	

† Values in each sub-table without a common lower case letter are significantly different at the $P < 0.05$ level of probability.


120
100
80
60
40
20
0
kg DM ha^{-1} day^{-1}
Growth
Net
Production
Senescence
0
500
1000
1500
2000
Herbage Mass kg OM ha^{-1}
0
1
2
3
4
5
6
7
8
Sward Height cm
0
1
2
3
4
5
Leaf Area Index

The influence of cutting and grazing management on herbage growth and utilisation

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SUMMARY

The rate at which herbage accumulates for harvesting represents the balance between the rate of growth of new plant tissue and the rate of loss of established tissue to senescence and decomposition. In theory both the rate of growth and the rate of loss can be controlled by cutting or grazing management, but in practice the effects of defoliation on the sward characteristics which determine these rates tend to be self-compensating.

The rate of herbage growth at a point in time may be limited either by the supply of assimilates from current photosynthesis and from plant reserves, or by the number, size and activity of growing points. Since photosynthetic activity and tillering respond differently to variations in sward management and in environmental conditions, growth responses can be difficult to predict, particularly in the long term. Assimilate production itself is not a simple function of leaf area, because adaptive changes in tiller population density and leaf age distribution in swards subjected to different managements all affect the photosynthetic efficiency of leaf tissue. Furthermore, any advantages to growth from the maintenance of a relatively high leaf area are likely to be accompanied by an increase in senescence losses.

As a consequence of these sward responses, substantial variations in management may have a relatively small impact upon the amount of herbage harvested, particularly from grazed swards. For a better understanding of the scope for manipulating net herbage accumulation

and harvesting efficiency, more information is needed on the effects of defined cutting and grazing managements on rates of tiller and leaf turnover in the sward, with associated measurements on tiller populations, on sward structure and morphology, and on leaf density. These variables can also influence the rate of herbage consumption by grazing animals and the nutritive value of the diet, so they form an important link between sward and animal studies.

INTRODUCTION

There has long been interest in the degree to which control of sward conditions can be used to influence herbage production and utilisation. However, despite an enormous amount of experimental work over the years, there is still controversy about the merits of alternative sward management strategies and their effects upon herbage production (e.g. Davidson, 1969; Hodgson and Wade, 1978). In this paper the objective is to review the evidence on the physiological processes influencing patterns of herbage growth and utilisation and their implications to sward management. The possible effects of interactions between defoliation strategy and limitations in the supply of either plant nutrients or water are not considered, though it is recognised that some of the inconsistencies in management effects may be attributable to interactions of this kind (Davidson, 1969). The dynamics of tissue turnover within the sward are first discussed briefly because of their importance to the argument.

TISSUE TURNOVER IN THE SWARD

The rate at which herbage accumulates in a sward protected from defoliation (NHA) represents the balance between the rate of growth of new tissue (G) and the rate of loss of mature tissue to decomposition (D):

$$NHA = G - D \qquad (1)$$

This simple approach can be elaborated to consider the flow through pools of living and dead tissue, when the flow from the 'live' to the 'dead' pool is described as senescence (S). Rates of G, D and NHA may be measured for the complete sward canopy, or restricted to the canopy above some defined limit for cutting or grazing. In continuously stocked swards the net rate of change in herbage mass is also affected by the rate at which herbage is consumed by grazing animals (C), so that:

$$NHA = G - (D + C) \qquad (2)$$

and NHA may well approach zero in many cases (e.g. Bircham and Hodgson, 1981).

In these terms G represents the potential production from a sward, and S and D might be regarded as measures of the inefficiency of the harvesting process. Rates of G, S and D may vary substantially across treatments (Morris, 1970; Tainton, 1974), but there is little information on the degree to which they can be manipulated independently. Measurements of NHA have been made routinely in pasture research for many years (Brown, 1954; Frame, 1981), but procedures for estimating rates of tissue turnover in the sward have not been widely used.

Estimates of G, S and D can be derived from measurements on grass tillers or clover stolons, or small areas of sward (Davies, 1981). Alternatively, since some 90% of the dry weight of the plant is made up of carbon compounds, measurements of carbon exchange may be used to estimate plant tissue fluxes (Parsons, 1981). In this case it is usual to think of the net retention of carbon by the plant (P_{nc}) as the balance between the gross uptake in photosynthesis (P_{gc}) and losses in respiration (R_{dc}):

$$P_{nc} = P_{gc} - R_{dc} \qquad (3)$$

The techniques are not strictly analogous, however, and care is needed in comparing estimates of ostensibly similar parameters derived from them.

SWARD ADAPTATION AND HERBAGE PRODUCTION

The concept of a sigmoid or asymptotic curve of accumulation of herbage mass against time, derived from growth analysis (Donald, 1951; Brougham, 1955, 1956) or carbon assimilation (Robson, 1973a, b) studies, is well established in the literature. Evidence of this kind led to the development of theories of sward management based on the maintenance of leaf area at intermediate levels, or its fluctuation within a range where light interception would be complete and rates of net carbon uptake or net herbage accumulation would be likely to be maximised (Davidson and Donald, 1958; Brougham, 1956). However, it has not always been easy to demonstrate that managements based on these principles actually result in an improvement in herbage production, particularly under grazing conditions (Holmes, 1962; Brown and Blaser, 1968). There is little information on the relationships between LAI, P_{nc} and NHA across swards managed in different ways, and it has perhaps been too readily assumed that the relationships established along growth curves can be applied between as well as within swards.

Most temperate swards are capable of a high degree of adaptation to treatments which are continued for any length of time (King, Lamb and McGregor, 1979), and frequently these changes appear to limit the impact of management upon the rate of herbage growth. Adaptive changes in tiller population density, sward canopy structure and photosynthetic efficiency are discussed in this section, but changes in the botanical composition of the sward, in rooting activity and in the partitioning of nutrients between shoot and root may all be implicated. NHA is likely to be affected by consequential changes in the rate of loss to senescence and decomposition, and these effects are also considered.

Tiller population density and sward structure

Net changes in tiller population density over time have been described

by many authors (Hunt and Brougham, 1966; Garwood, 1969; Kays and Harper, 1974), but patterns of tiller development and loss are less well documented despite the fact that tiller turnover is a dynamic process (Langer, Ryle and Jewiss, 1964). The development of new tillers in a sward is unlikely to be limited by the supply of tiller buds (Alberda, 1966; Davies, 1977). Development is stimulated by defoliation, though the number of new tillers initiated, and the rate at which they develop, is likely to be strongly affected by sward conditions both before and after defoliation (Jewiss, 1972). The loss of tillers is increased by both severe shading (Kays and Harper, 1974) and by severe defoliation (Brougham, 1959; Smith, Arnott and Peacock, 1971). Patterns of response appear to be similar for most sward-forming grass species and for white clover, though tiller population density and the rate of tiller turnover may differ between plant genotypes (e.g. Davies, 1977).

Changes in tiller density can be extremely rapid, often over short periods of time (Brougham, 1960; Garwood, 1969; Langer, et al 1964), though it may be easier to depress than to increase populations in the short term. Grant, King, Barthram and Torvell (1981b) found that the rate at which tiller populations diverged in swards maintained at different levels of herbage mass was much lower before the summer solstice when light conditions in the field were steadily improving, than after the solstice when they were steadily declining, though all the swards were tillering actively. The degree to which differences in the physiology of the plant were implicated is not clear.

Tiller populations tend to increase as the frequency of defoliation increases (Table 1), and are maintained at a higher level under continuous stocking management than under rotational grazing at comparable stocking rates (Hodgson and Wade, 1978). The influence of severity of defoliation is more complex, populations tending to be greatest at intermediate levels

of defoliation, but the pattern of response is sensitive to both sward and climatic conditions at the time of defoliation (Brougham, 1960; Jewiss, 1972; Grant et al, 1981a, b). Tiller numbers on continuously stocked L. perenne/Poa annua/T. repens swards have tended to increase progressively with reductions in herbage mass down to levels of about 700 kg ha^{-1} OM, measured to ground level, but to fall sharply with further reductions in herbage mass (Bircham and Hodgson, 1981). Under these conditions, peak tiller numbers can be in the range from 40,000 to 60,000 m^{-2} (Grant et al, 1981b; Bircham and Hodgson, 1981; Collett and Lewis, 1981).

/Table 1 here/

In our studies the relationship between the tiller population density (x) and individual tiller weight (y) across swards has approximated closely to the $-3/2$ relationship demonstrated by White and Harper (1970) and Kays and Harper (1974) for a range of herbaceous plant communities allowed to grow undisturbed in full light. This relationship held true down to levels of herbage mass of the order of 700 kg ha^{-1} OM, the value of the exponents derived from four studies lying in the range from -1.2 to -1.7, but broke down as the tiller population started to decline at lower herbage mass. This may be taken as an indication of the limit of adaptability of the swards in question.

In addition to changes in tiller population and average tiller weight, the structure of the sward canopy also adapts rapidly to defoliation management. Increases in the frequency and severity of defoliation of a sward are likely to lead to a reduction in pseudostem length and a reduction in tiller and leaf angle resulting in an increasingly prostrate sward (Kydd, 1966; Jackson, 1974; Grant and King, unpublished data - see Table 2).

/Table 2 here/

Leaf area and photosynthesis

The increase in tiller population density and the decline in leaf angle which occur in frequently and closely defoliated swards maintain a greater degree of light interception than would otherwise be the case (King et al, 1979). Also, the relatively high irradiance levels in the base of closely defoliated swards and the increase in the proportion of young to old leaf are likely to result in an increase in the photosynthetic efficiency per unit of leaf tissue (Woledge, 1977). The effects of these changes are illustrated in Fig. 1 which compares the relationships between LAI and P_{nc} measured (a) during regrowth in intermittently cut swards (King et al, 1979), and (b) across a series of continuously stocked vegetative swards maintained at different levels of LAI under grazing by either sheep or cattle (King, unpublished data). The regression of P_{nc} on LAI with time in an intermittently defoliated sward is nearly always curvilinear (Leafe, 1972; King et al, 1979), whereas rectilinear relationships appear to be common, at least between LAI 1 and 6, on continuously stocked swards. The latter characteristically have substantially higher values of P_{nc} than the former at low LAI, but their photosynthetic advantages tend to decline progressively with increasing LAI (Fig. 1). The degree of compensation possible on a short sward will depend in part upon the effectiveness of light interception, but our evidence (King, unpublished data), indicates that as much as 80% of incident light can be intercepted in continuously stocked swards with an LAI as low as 2.0.

/Fig. 1 here/

The linear regression coefficients of P_{nc} on LAI established for vegetative swards in these and other studies at HFRO usually lie in the range 0.67-1.08 g m^{-2} h^{-1} CO_2 at 320 Wm^{-2}. In one study, however, the coefficient declined from 0.66 to 0.24 g m^{-2} h^{-1} CO_2 over a period of about 30 days when the swards were adjusting to treatment (Fig. 2).

Tiller population density increased rapidly over the same period at low LAI, resulting in an improvement in photosynthetic efficiency, whereas there was a progressive decline in the efficiency of the ageing leaf tissue at high LAI. The degree to which this evidence is indicative of a progressive change with time is not clear, but it demonstrates the potential for adaptive changes.

/Fig. 2 here/

Losses to senescence and decomposition

Any leaf on a grass tiller has a limited life span before the onset of senescence results in a progressive loss in weight. Thus, any management designed to achieve high LAI and high P_{gc} by extending the defoliation interval or reducing the severity of defoliation carries with it the risk of an increase in senescence losses. So long as the interval between defoliations does not exceed 2-3 leaf appearance intervals (3-4 weeks in temperate swards, depending on the time of year) the amount of tissue lost to senescence above cutting height is likely to be small, but substantial amounts of tissue may well be lost below cutting height (Morris, 1970). Under grazing conditions more of the sward canopy is in theory accessible for defoliation, but in most circumstances animals will consume relatively small amounts of senescent tissue (Hamilton, Hutchinson, Annis and Donelly, 1973; Barthram, 1980) so that here, too, any tissue reaching the stage of senescence is effectively a loss to the system.

Losses to senescence and decomposition increase to a maximum during the uninterrupted growth of a sward (Robson, 1973a; Hunt and Brougham, 1966; Hunt, 1970). They are also likely to be directly related, across managements, to herbage mass and to the amount of stubble remaining after defoliation (Campbell, 1964; Wade, 1979). Thus, any advantages in P_{nc} and herbage growth to be derived from a high LAI (Fig. 1) are likely to be at least partially counterbalanced by increased losses of

mature tissue, and the effects of variations in both the frequency and severity of defoliation in grazed and cut swards may be due as much to changes in the balance between rates of growth and decomposition as to changes in growth per se (Tayler and Rudman, 1966; Anslow, 1967; Morris, 1970; Tainton, 1974).

STABILITY OF HERBAGE PRODUCTION IN TEMPERATE SWARDS

It is clear that adaptive changes in tiller population and sward structure can modify the influence of frequent or severe defoliation on leaf area, and can enhance both the photosynthetic efficiency of leaf tissue and the number of growth sites within the sward. These effects appear to be progressive with time. Any residual differences in rates of herbage growth can be further eroded by the tendency for between-treatment variations in G and D to be correlated. These effects are quite large enough to explain why managements which would be expected to create marked differences in LAI may have only a limited impact upon NHA. In practice the degree of adaptation may be greater in grazed than in cut swards (Hodgson and Wade, 1978), but few long-term sward studies have provided information in sufficient detail to allow an assessment of the magnitude and the relative importance of the changes which occur. The results of two recent studies at HFRO are used here to illustrate the point, and to develop a view of the stability of net herbage production in temperate swards. Both studies involve an approximation to continuous stocking management, one under grazing conditions and one involving frequent clipping treatments.

/Fig. 3 here/

In a study on mini-swards of L. perenne in a glasshouse which were maintained at predetermined levels of LAI by weekly clipping for six weeks, King and Grant (unpublished data) found that NHA reached a maximum over the range from LAI 3.5 to 4.5, and declined at both lower and higher

LAI (Fig. 3). Bircham and Hodgson (1981), working with mixed L. perenne/ Poa annua/T. repens swards maintained at predetermined levels of herbage mass under continuous but variable stocking with ewes and lambs for 3-4 months, found that net herbage production (= G-S, in conditions where the balance was consumed by the sheep) was maximal at a maintained herbage mass of about 1250 kg ha^{-1} OM (LAI 3) but was relatively stable over the range from 1000 kg to 2000 kg ha^{-1} OM (LAI 2-5) (Fig. 4). This pattern of response in net production was the result of a linear increase in S over the range of herbage mass examined, superimposed on values of G which increased relatively slowly above a herbage mass of 1200 kg ha^{-1} OM (LAI 3). In other field studies at HFRO on swards under comparable management (Grant, unpublished data; Grant and King, unpublished data), values of G have tended to increase progressively over comparable range of herbage mass, but effects on net herbage production have again been minimal because of compensating changes in S.

/Fig. 4 here/

The results of all these studies demonstrate that the rate of net herbage production is remarkably stable across a range of maintained sward conditions although the adaptive changes in tiller population, sward structure and the photosynthetic efficiency of leaf tissue contributing to stability may have differed in different circumstances (Bircham and Hodgson, 1981; Grant et al, 1981a, b). Under grazing conditions, the direct effects of an increase in the efficiency of defoliation may be reinforced by more efficient recycling of plant nutrients in dung and urine, and possibly by treading effects upon tillering activity, but these latter factors would not influence herbage production on cut swards. The lower limit of adaptation, as noted earlier, appears to be marked by a substantial fall in tiller population similar to that reported by Hodgson and Wade (1978) and Wade (1979) for rotationally grazed swards, and a breakdown in the inverse relationship between

tiller size and population density.

These results can be interpreted as an inevitable consequence of the management required to maintain specified LAI values in the sward. From first principles, the proportion of new leaf tissue which must be removed to maintain a given LAI decreases linearly from a value approaching 1.0 as LAI approaches zero, to a value approaching zero at maximum LAI. Using the results obtained by Robson (1973b) for a seedling sward in uninterrupted growth, Fig. 5 illustrates the relationships between LAI and (a) the rate of gross carbon assimilation per unit ground area, and (b) the rate at which carbon would have to be harvested in order to maintain a specified LAI (determined as the product of P_{gc} and the proportion of leaf harvested). There are reservations about this use of results of measurements on a sward in continuous growth, because adaptive changes of the kind described earlier for continuously stocked swards would not occur, and patterns of tissue growth and senescence may be out of phase (Parsons and Robson, 1981). Nevertheless the similarities between Figs. 4 and 5 are clear. Similar predictions can be derived from the results of other experiments (Woledge and Leafe, 1976) and all analyses indicate that the amount of tissue which could be harvested from a sward under steady-state management would be maximised in the range LAI 3-4.

/Fig. 5 here/

The limited impact of variations in sward conditions upon net herbage production in our studies raises again the question of the potential value of intermittent defoliation, but in a different context. Is it possible that deliberately induced fluctuations in LAI will allow some gain in herbage production? Early results are not encouraging. Thus, Bircham (1981) found that a previously hard-grazed sward allowed to grow to a new steady state at higher herbage mass in the autumn gave no higher net herbage production than companion swards maintained throughout at either the low or the high level. Grazing a sward down from the high to

the low mass depressed net herbage production. Grant et al (1981b) suggest that there may be scope for a more favourable response at other times of the year, but this suggestion has not yet been tested. Leafe, Parsons, Stiles and Collett (1979) also observed little difference in the estimates of total season's net carbon accumulation in swards either cut monthly or grazed to maintain an LAI of 2-3, and concluded that this was due primarily to the fact that higher losses of carbon in respiration balanced out the higher rate of carbon assimilation on the sward cut monthly.

DETERMINANTS OF HERBAGE GROWTH AND UTILISATION

Throughout this review the sward has been considered as a dynamic entity, in which the processes of tissue production and loss occur simultaneously and almost continuously. Management effects on NHA may operate through their influence on the rate of growth of new plant material, the rate of loss of mature tissue or, since they are frequently not independent, some combination of the two effects. The objective of management should therefore be to optimise the balance between the two rather than, as has often been the case, to attempt to maximise growth rate.

It has been conventional to regard assimilate supply as the major determinant of plant growth, and many theoretical studies of the influence of sward management on herbage production start from this assumption (de Wit, Brouwer and Penning de Vries, 1971; Sheehy, Cobby and Ryle, 1979). However, the evidence reviewed above supports the view expressed by Hodgson and Wade (1978) and Wade (1979) that herbage production is often likely to be influenced by variations in the numbers and activity of the growth sites in a sward. For example, stability in rates of herbage growth and net accumulation across a series of treatments appears to be dependent upon compensating changes in tiller population and tissue turnover per tiller, and a marked depression in growth per unit area is only apparent in

treatments which result in a substantial depression in tiller numbers (Wade, 1979; Bircham and Hodgson, 1981). The need for objective information on the factors likely to determine the relative importance of the effects of limitations to assimilate supply or assimilate demand on plant production has been emphasised on previous occasions (e.g. Watson, 1971), but there is little clear evidence for grass swards.

In fact the two views are not so much contradictory as complementary, and the relative importance of growth site activity and assimilate supply might be expected to change during a cycle of growth or as environmental conditions change. Nevertheless, the management requirements for a high current supply of assimilate (dependent upon a high current or previous LAI) and those for the maintenance of a future supply of assimilate (dependent upon the maintenance of a vigorous tiller population) may be seen to be in conflict. For example, managements designed to maintain high LAI can clearly have an adverse effect upon tiller populations in the medium and long term.

The factors influencing rates of herbage growth and loss are inter-related to a degree which makes it difficult to assess their relative importance in specified circumstances, and hence to predict the influence of particular management strategies on the balance between them. The matter is further complicated by the fact that the sward characteristics affecting photosynthetic activity and tillering activity are likely to have an impact on the overall efficiency of a grassland system through their influence on herbage intake and nutritive value, grazing efficiency and, ultimately, animal production. Thus, herbage intake is likely to decline as the ratio of leaf to stem increases and the digestibility of leaf tissue declines with increasing maturity (Hodgson, Rodriguez Capriles and Fenlon, 1977), and as the depth of the leaf layer in the sward and the bulk density of leaf decline (Barthram, 1980; Hodgson, 1981). In general terms, managements designed to maintain high leaf area are likely

to reduce herbage digestibility and leaf bulk density, and increase the depth of the leaf layer, relative to managements designed to encourage high tiller population densities.

CONCLUSIONS

The evidence reviewed above illustrates the adaptability of temperate swards, and supports the view of Hodgson and Wade (1978) that there may be relatively little scope for improving the amount of herbage harvested per unit of land area, at least under grazing management. However, this is not to suggest that there is no basis for sward control. The results indicate in relatively objective terms the circumstances in which the productive potential of a sward is likely to be impaired, and they provide a basis for assessing the influence of managements designed to maintain long-term sward stability through the maintenance of substantial tiller populations. An adequate understanding of the scope for achieving worthwhile improvements in the amount of herbage harvested per unit area of grassland is dependent upon a better appreciation of ways in which adaptive changes can influence tiller populations and tissue flows under field conditions, and the limitations to adaptation. This in turn requires the adoption of a wider range of sward measurements and a more critical approach to sward responses than has frequently been the case in the past.

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Table 1. The influence of the number of cuts per annum on tiller population density (tillers m^{-2}) in a mixed *L. perenne*/*A. tenuis*/*T. repens* sward†. (Bircham, (unpublished data).

	Cut to 1 cm from:-			
	12 cm	8 cm	4 cm	2 cm
No. cuts per year	3	4	8	17
Tillers m^{-2}	11,400	15,300	17,700	18,100

	Cut to 3 cm from:-		
	12 cm	8 cm	5 cm
No. cuts per year	3	4	10
Tillers m^{-2}	9,300	12,600	15,400

SE of treatment mean ± 1220

† Measurements made in spring, after treatments had been imposed for one year. Results shown are means of four replicates.

Table 2. The relationship between LAI and pseudostem length (mm) in micro-swards of L. perenne (Grant and King, unpublished data).

	Swards cut weekly to LAI :-				
	1	2	3	4	5
After six cuts	23 ± 0.6	25 ± 0.8	31 ± 1.2	40 ± 1.1	46 ± 0.8
After all swards cut to LAI 1 †	23 ± 0.8	23 ± 0.8	27 ± 1.1	31 ± 1.1	35 ± 0.9

† Values after 15 days regrowth and 1.6-1.8 new leaves per tiller

LEGENDS FOR FIGURES

Figure 1. The relationships between LAI and net canopy photosynthesis (g m^{-2} h^{-1} CO_2 at 320 Wm^{-2}) for (a) swards over periods of regrowth following regular cutting (A) weekly to 2 cm, (B) every three weeks to 4 cm, and (C) weekly to 4 cm (solid lines), and (b) swards continuously stocked by either sheep or cattle to maintain different LAI levels (broken lines). For details of results from cut swards see King et al (1979).

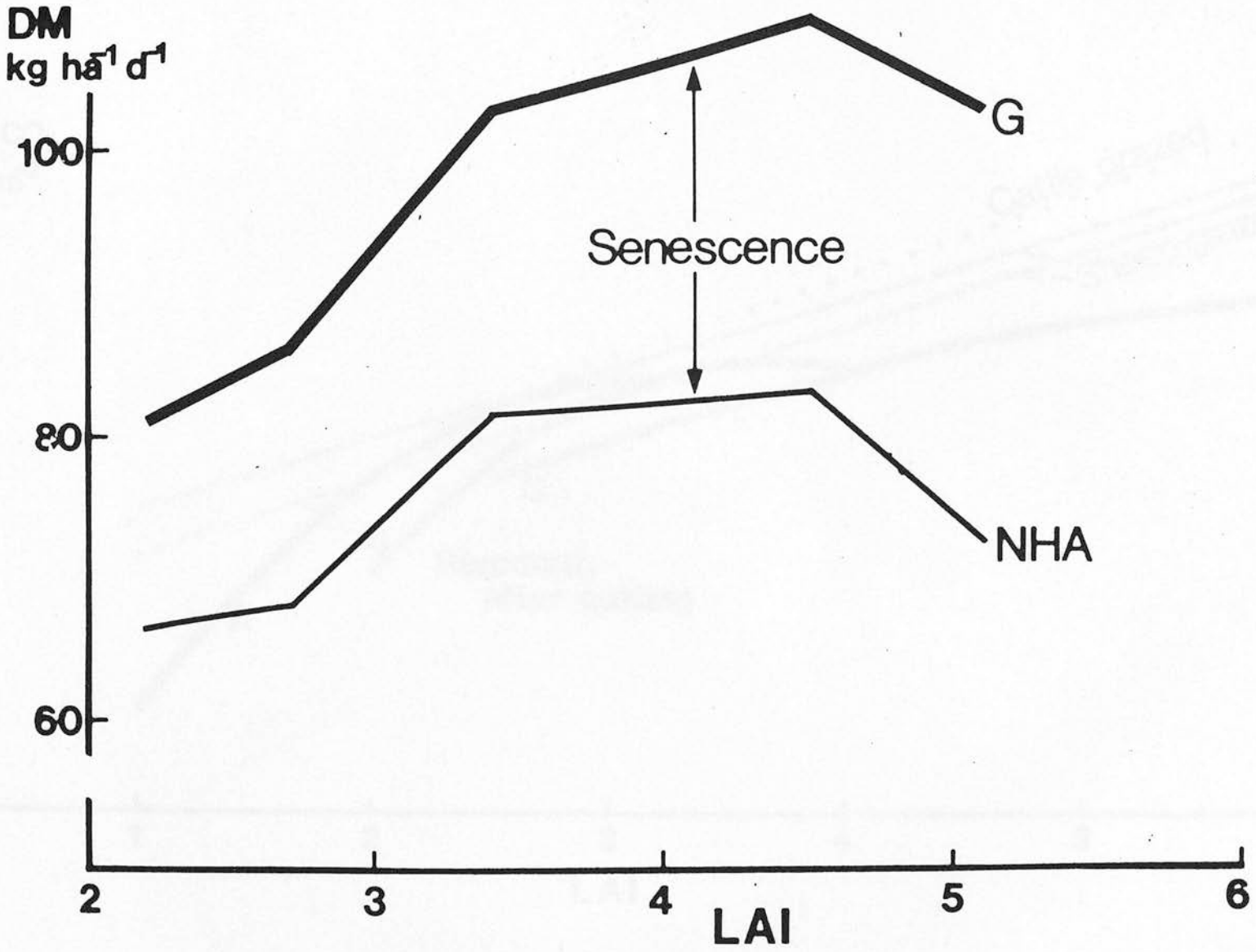
Figure 2. The relationships between LAI and net canopy photosynthesis (g m^{-2} h^{-1} CO_2 at 320 Wm^{-2}) measured in July and again in August/September on swards continuously stocked by sheep from mid June.

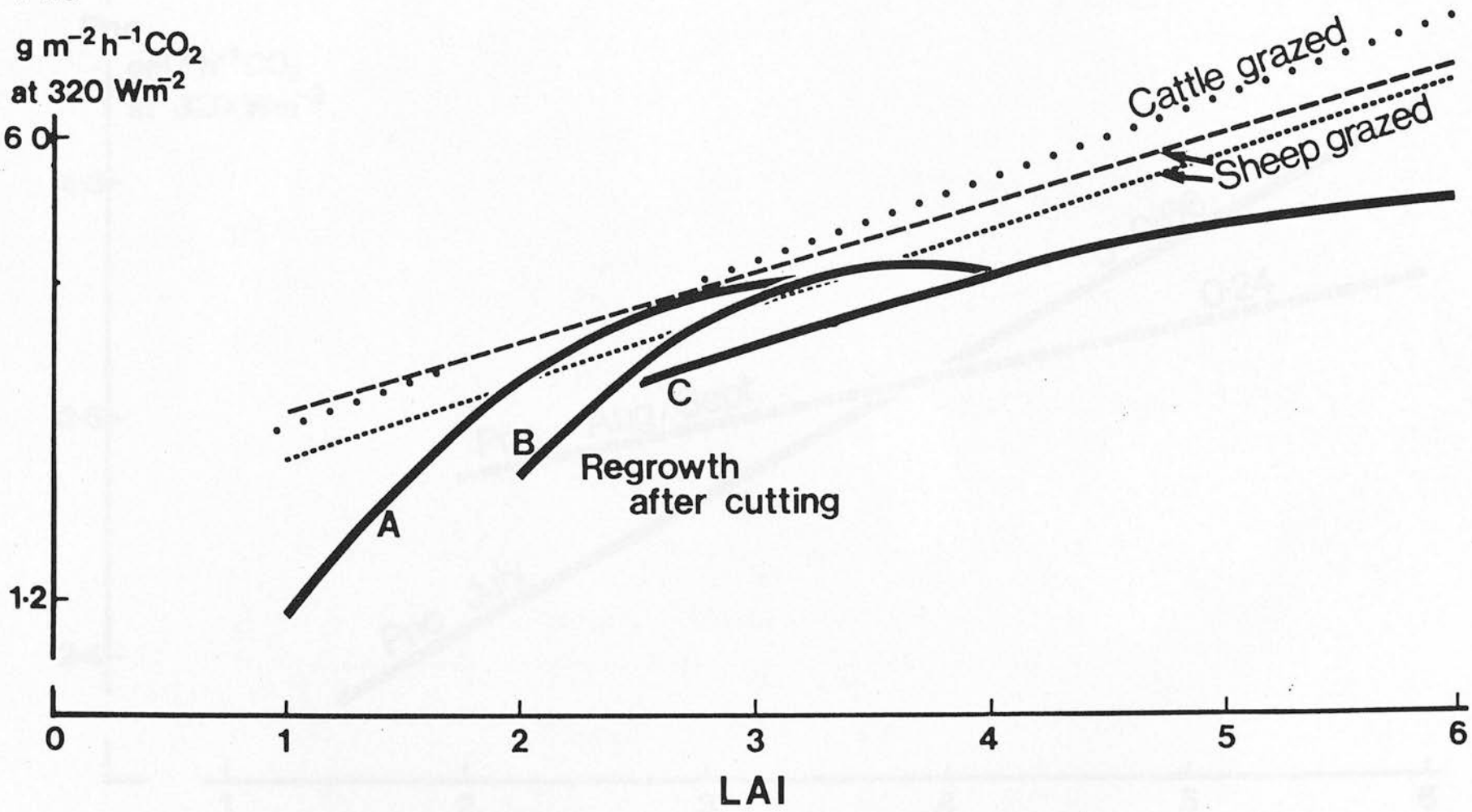
Figure 3. The relationships between LAI and rates of herbage growth (G) and net accumulation (NHA) (kg $ha^{-1}d^{-1}$ DM) in swards cut weekly to specified LAI values (Grant and King, unpublished results).

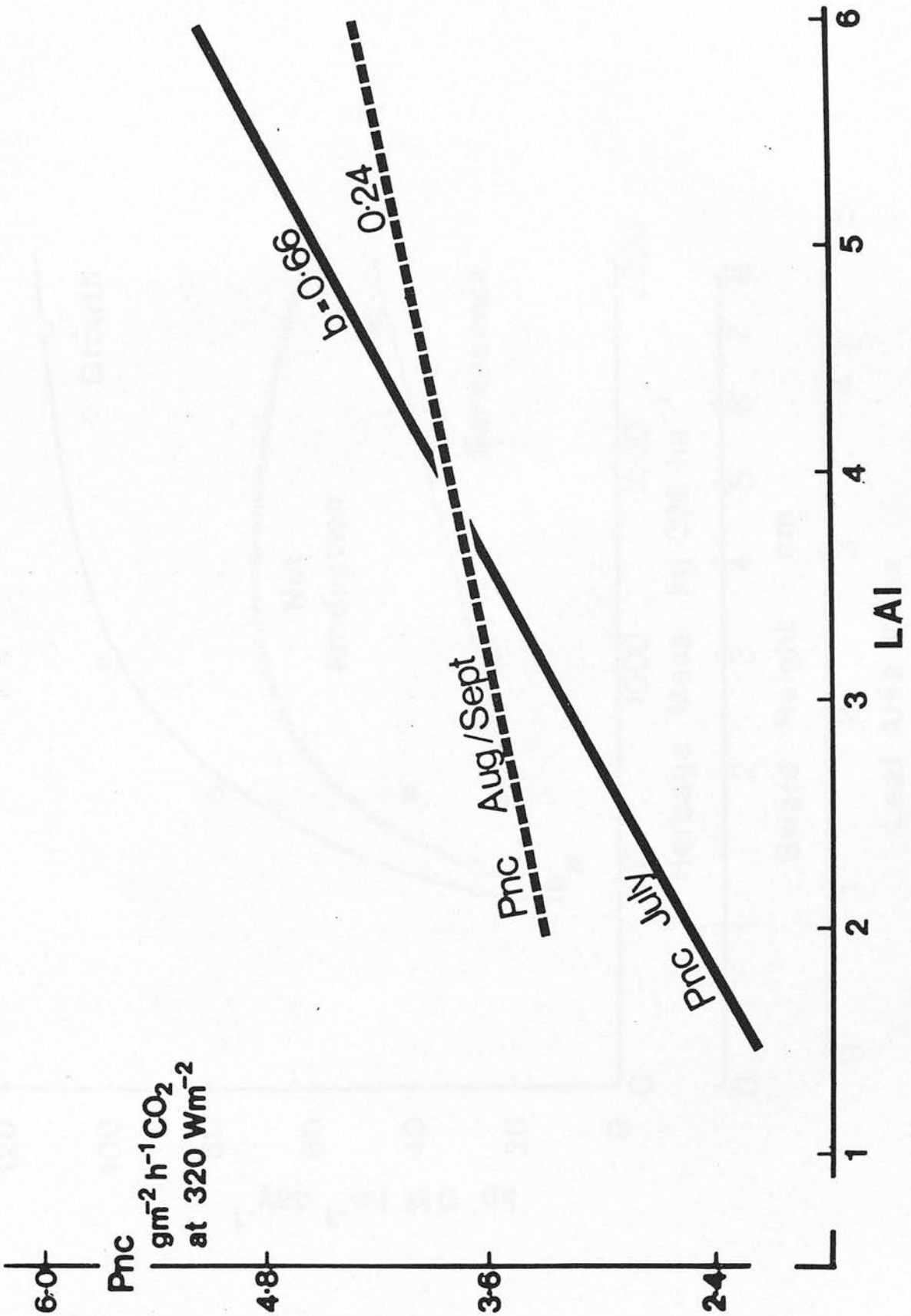
Figure 4. Relationships between herbage mass (kg ha^{-1} OM), sward height (cm) and LAI, and rates of herbage growth (G), senescence (S) and net production (NP) (all kg $ha^{-1}d^{-1}$ DM) in swards continuously stocked by sheep (Bircham and Hodgson, 1981).

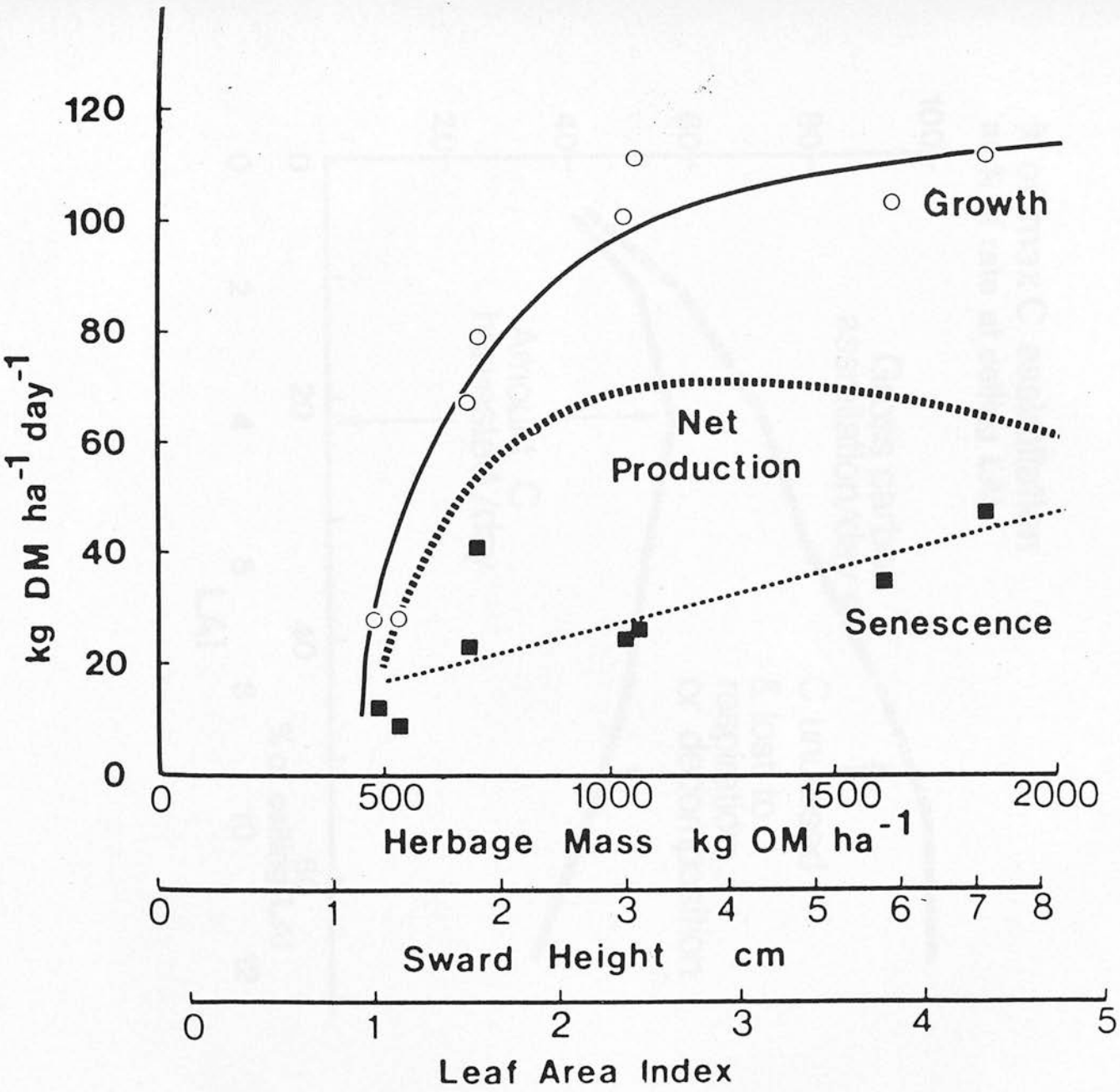
Figure 5. The relationships between LAI and (a) the rate of gross carbon assimilation (P_{gc}), and (b) the rate at which carbon would have to be harvested in order to maintain a specified LAI (both expressed as % of maximum P_{gc}). The rate of harvesting carbon is the

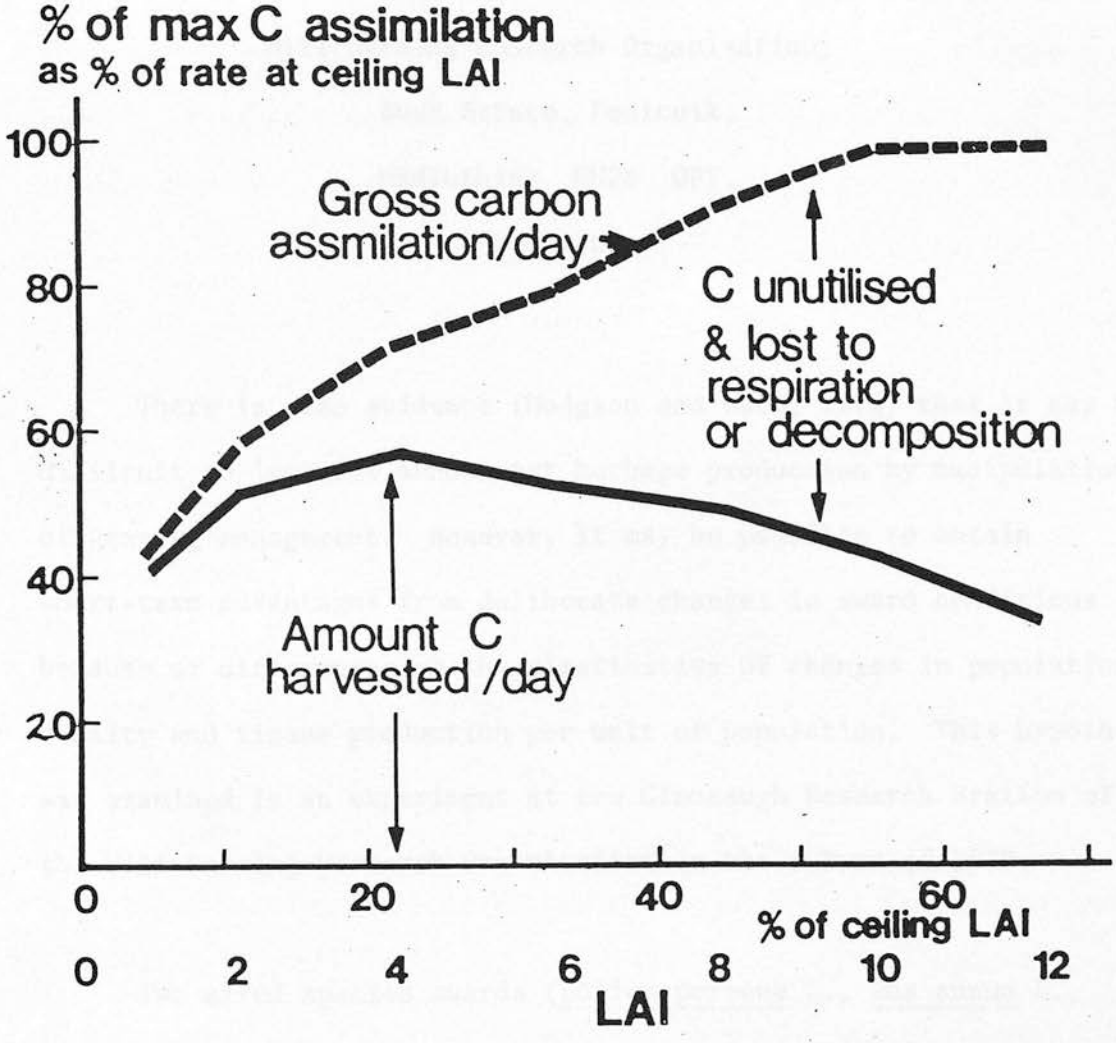
product of P_{gc} and the proportion to be harvested to maintain LAI, where this proportion approaches 1.0 as LAI approaches zero, and approaches zero as LAI approaches LAI_{max} (see text).


DM
kg ha⁻¹ d⁻¹
100
80
60
G
Senescence
NHA
2
3
4
5
6
LAI


Pnc
g m⁻² h⁻¹ CO₂
at 320 Wm⁻²
6·0
1·2
Cattle grazed
Sheep grazed
A
B
C
Regrowth
after cutting
0
1
2
3
4
5
6
LAI


Pnc
gm⁻² h⁻¹ CO₂
at 320 Wm⁻²
6·0
4·8
3·6
2·4
1
2
3
4
5
6
LAI
Pnc July
Pnc Aug/Sept
b=0·66
0·24


120
100
80
60
40
20
0
kg DM ha-1 day-1
Growth
Net
Production
Senescence
0
500
1000
1500
2000
Herbage Mass kg OM ha-1
0
1
2
3
4
5
6
7
8
Sward Height cm
0
1
2
3
4
5
Leaf Area Index


% of max C assimilation
as % of rate at ceiling LAI
100
80
60
40
20
Gross carbon
assmilation/day
C unutilised
& lost to
respiration
or decomposition
Amount C
harvested /day
0
20
40
60
% of ceiling LAI
0
2
4
6
8
10
12
LAI

The effects of a change in herbage mass on herbage growth, senescence and net production rates in a continuously stocked mixed species sward.

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There is some evidence (Hodgson and Wade, 1978) that it may be difficult to increase annual net herbage production by manipulation of grazing management. However, it may be possible to obtain short-term advantages from deliberate changes in sward conditions because of differences in the elasticities of changes in population density and tissue production per unit of population. This hypothesis was examined in an experiment at the Glensaugh Research Station of the Hill Farming Research Organisation in the autumn of 1979.

Two mixed species swards (Lolium perenne L., Poa annua L., Trifolium repens L.) which had been maintained at 700 - 1100 kg ha^{-1} OM (L) and 1700 - 2100 kg ha^{-1} OM (H) herbage mass under continuous but variable stocking with sheep from May to mid-August

t/ On study leave from Whatawhata Hill Country Research Station, Hamilton, New Zealand.

were split. One half of L was permitted to grow until a mass similar to that of H was achieved (LH), and one half of H was grazed down to L (HL) over a period of 3-4 weeks. The remaining half of each of the original swards was maintained (LL and HH) in as near steady state as possible by continuous but variable stocking with sheep and when the changes were complete, all four swards were maintained constant for a further three weeks. Estimates of rates of herbage growth, senescence and net production were made from repeated measurement on individual tillers and stolons in the last two weeks of this period. Fertiliser was applied in mid-April at a rate equivalent to 123 kg N, 37 kg P and 37 kg K ha^{-1} respectively, followed by nitrogenous fertiliser alone in mid-July at 40 kg ha^{-1} N and a compound fertiliser in mid-August equivalent to 49 kg N, 25 kg P and 25 kg K ha^{-1}.

The population densities of individual plant units (grass tillers and stolon growing points) were highest in LL and lowest in HL (Table 1). Mean tissue growth and senescence rates (μg $tiller^{-1}$ day^{-1} DM) for individual ryegrass tillers only are given in Table 1, these results being representative of the trends in the other species. Both growth and senescence rates on individual tillers were highest in HH and LH, and lowest in LL and HL. Combined species growth and senescence rates per unit area, calculated from corresponding rates per unit of population and population densities for individual species, were highest in LH and lowest in HL, with the rates for LL and HH intermediate (Table 1). Net herbage production rates per unit area

were significantly lower in HL than in the other three swards.

The response to alteration in herbage mass was rapid at the individual plant unit level but population density changes were slower. The higher growth rate per unit area in LH compared to LL occurred because a higher growth rate per individual plant unit more than offset a decline in population density, whereas the higher growth rates in LH than in HH, and in LL than in HL, were due primarily to differences in population density. The same reasoning can be applied to explain the observed effects on senescence rates per unit area except that the higher senescence rates in the LH compared to HH were due to differences in both individual plant unit senescence rate and population density. The high senescence rate in LH reflects a higher lamina death rate combined with loss of whole plant units, which would presumably continue until a stable population similar to that of the HH sward was established.

In this experiment deliberate changes in sward conditions did not result in any increase in net green herbage accumulation over swards maintained in a steady state. In the sward allowed to grow from low to high mass, the increase in senescence losses balanced any improvement in herbage growth rate, and in the sward reduced from high to low mass the increase in plant unit population density was not nearly fast enough to offset the reduction in the rate of growth per unit. It remains to be seen whether these conclusions are of more general application, for example to different seasons or to different methods of sward management.

REFERENCES

Hodgson, J. and Wade, M.H. (1978). Grazing management and herbage production.

Proceedings of the British Grassland Society Winter Meeting, 1978, pp. 1.1-1.12.

Table 1. The effects of short term change in maintained herbage mass on population density (units m^{-2}); growth and senescence rates for individual ryegrass tillers ($\mu g\ tiller^{-1}\ day^{-1}$ DM); combined species growth, senescence and net production rates ($kg\ ha^{-1}\ day^{-1}$ DM).

	Treatment[t]				
	LL	HH	LH	HL	SE of Mean
Population	63800 a[++]	29500 c	47400 b	23900 c	3870
Ryegrass Tillers					
Growth	121 b	219 a	224 a	105 b	15.6
Senescence	39 b	78 ab	114 a	44 b	15.8
Combined Species					
Growth	59 b	51 b	73 a	19 c	4.6
Senescence	24 b	22 b	40 a	8 c	3.8
Net Production	35 a	29 a	34 a	11 b	6.2

t/ See text.

++/ Values in rows without a common lower case letter are significantly different at the $P \leqslant 0.05$ level of significance.